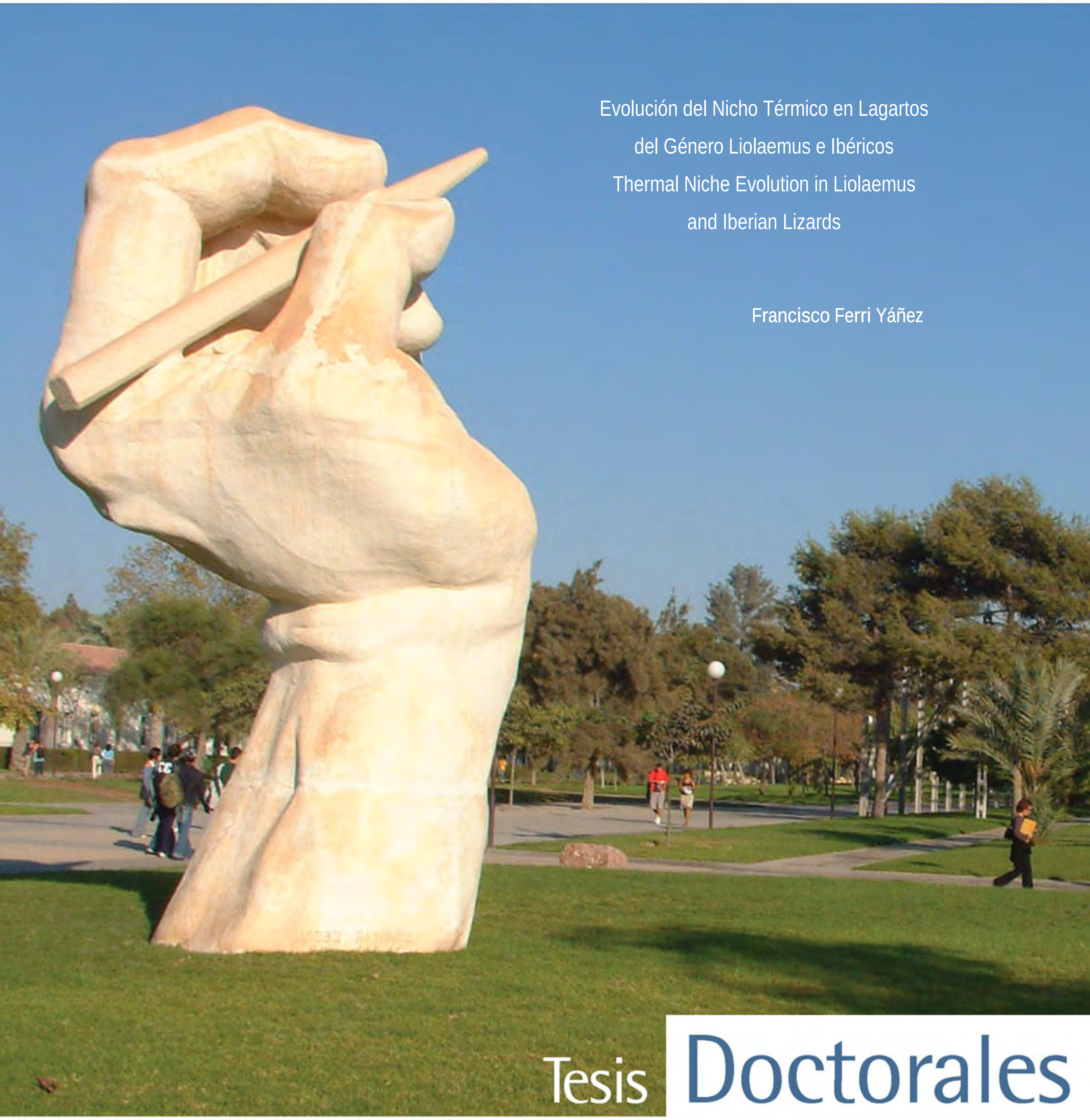

Evolución del Nicho Térmico en Lagartos del Género Liolaemus e Ibéricos

Thermal Niche Evolution in Liolaemus and Iberian Lizards

Francisco Ferri Yáñez

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Evolución del nicho térmico en lagartos del género Liolaemus *e ibéricos*

FRANCISCO FERRI YÁÑEZ

Tesis presentada para aspirar al grado de:
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DOCTORADO EN BIODIVERSIDAD Y CONSERVACIÓN

Dirigida por:

Dr. Miguel Bastos Araujo	Dr. Pablo Marquet
Departamento de Biogeografía y Cambio Global	Departamento de Ecología
Museo Nacional de Ciencias Naturales (CSIC)	Pontificia Universidad Católica de Chile

Bajo la tutela académica de:
Dr. José Ramón Verdú Faraco
Instituto Universitario de Investigación - CIBIO
Universidad de Alicante

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A mis abuelos,
José Yáñez Verdú y María Llorens Francés

A mis padres,
Francisco Ferri Llorens y Amelia Yáñez Tortosa

Nota acerca del idioma:

En la redacción de la presente tesis doctoral se han utilizado dos idiomas: español e inglés. Los apartados *Introducción, Justificación y objetivos de la tesis* han sido escritos en castellano, mientras que los Capítulos 1–4 aparecen íntegramente en inglés. Se incluyen en ambos idiomas los siguientes apartados: *Contenidos*, *Resumen de la tesis* y *Conclusiones*.

Note about the language:

This PhD Thesis has been written in two languages: Spanish and English. *Introduction, Rationale and Objectives*, have been written in Spanish, while *Chapters 1-4* are entirely in English. The following sections are included in both languages: *Contents*, *Abstract*, and *Conclusions*.

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"… species of the same genus have usually, though by no means invariably,
some similarity in habits and constitution, and always in structure..."

Charles Darwin - 1859
On the Origin of Species. Chapter III

CONTENTS
Contenidos

THESIS ABSTRACT

Environmental changes have shaped to a great degree the current patterns of biodiversity. In the current context of fast environmental and climatic change, there is a need to forecast how species will react to it. Species have been evolving in changing environments and continue to do so but the speed at which climate change is happening now is much faster than it normally happened before the industrial era. Due to that, it is generally assumed species will not have time to adapt so their niches will remain constant. Nevertheless there are examples of fast niche shifts and even evolutionary adaptations during short time spans so that assumption is not tested.

The aims of this PhD thesis are to determine how conserved is thermal physiology in relation to temperature along the phylogeny and try to evaluate how plausible is for organisms to adapt to increasing temperatures. For that I use a highly diverse group of South American iguanid lizards as model organisms in which I measured thermal ecophysiological traits and for which I construct a time calibrated molecular phylogeny. I also use fourteen species of Iberian lacertid lizards to explore the possibility of using mathematically modeled physiological temperatures as variables for bioclimatic envelope models.

In **Chapter 1** I analyzed the thermal tolerances of a large number of terrestrial organisms and found that heat tolerances are strongly conserved while cold tolerances vary markedly in a pattern that is consistent across taxa for ectotherms, endotherms and plants. I argue that this asymmetry causes the thermal component of the fundamental niche to overlap between species more than previously expected. Also, as a consequence, estimated niches for cold-adapted species may underestimate their upper thermal limits and potentially exaggerated the risk from climate change. On the other hand it is unlikely that species which are close to their upper thermal limit will increase their heat tolerance.

In **Chapter 2** I focus on *Liolaemus* lizards. Here I constructed a time calibrated phylogeny and analyzed the diversification patterns of the genus in relation to climate and geological history. I set the origen of diversification of the group further back in time, questioning hypothesis of Andean vicariance as a trigger for their diversification. The general pattern of diversification suggests a gradual opening of new niches. Moreover, I find that the group shows different diversification patterns on both sides of the Andean Cordillera, and that the diversification of the Argentinian group (subgenus *Eulaemus*) is related to global temperature change.

On the **Chapter 3**, I incorporated thermal physiological traits to the phylogenetic analysis and estimated how fast they have been changing in time. I show that, to keep the pace of currently increasing temperatures, traits would have to evolve four or five orders of magnitude faster than the fastest rate observed. Phylogenetic comparative analysis shows that *Liolaemus* thermal traits are conserved beyond what is expected by Brownian Motion alone and that thermal preferences and field temperatures show more phylogenetic inertia than thermal limits. All this makes unlikely that evolutionary adaptation of thermal

physiological traits may play a signifficant role in their response to climate change. In addition, I explore the possibility that comparative methods can be used to estimate missing traits in species that have not been measured.

Finally, in **Chapter 4** I tested the claim that bioclimatic envelope models should be fitted with direct variables. I used a dynamic climate downscaling of the Iberian Peninsula to calculate operative temperatures and use them, and air temperatures, to create bioclimatic envelope models of fourteen lacertid lizards. I show that model performance is similar when using operative or air temperatures and that temporal trends during the second half of the twentieth century do not differ significantly between variables. Our study points towards that the use of proximal variables does not always possitively affects the quality of a model.

RESUMEN DE LA TESIS

Los cambios ambientales han moldeado en gran medida los patrones de diversidad biológica. En el contexto actual de rápidos cambios ambientales y climáticos se hace necesario predecir cómo reaccionarán las especies a estas presiones. Las especies han evolucionado en ambientes cambiantes y continúan haciéndolo. Sin embargo, la velocidad a la que cambia el clima en estos momentos es mucho más elevada a la de cambios climáticos anteriores a la revolución industrial. Debido a ello, se suele asumir que las especies no tendrán mucho tiempo para adaptarse, por lo que sus nichos permanecerán estables. No obstante, hay ejemplos de cambios rápidos del nicho e incluso de adaptaciones evolutivas durante breves periodos de tiempo, porque lo que esa asunción necesita ser testada.

Los objetivos de esta tesis doctoral son determinar hasta qué punto está conservada la ecofisiología térmica a través de la filogenia e intentar evaluar la capacidad de adaptación de los organismos al incremento de temperatura. Para ello he utilizado un grupo altamente diverso de lagartos iguánidos de Sudamérica como modelo de estudio, en el que he medido rasgos térmicos ecofisiológicos y para los que construimos una filogenia molecular calibrada con el tiempo. Además, he utilizado catorce species de lacértidos ibéricos, para explorar la posibilidad de utilizar temperaturas fisiológicas modelizadas matemáticamente como predictores en modelos bioclimáticos.

En el **Capítulo 1** analicé las tolerancias térmicas de gran número de organismos terrestres y encontré que las tolerancias al calor están muy conservadas, mientras que las tolerancias al frío varían de forma notable, siendo este patrón consistente para ectotermos, endotermos y plantas. Discuto que esta asimetría hace que el componente térmico del nicho fundamental se superponga entre muchas más especies de lo esperado. Además, en consecuencia, los nichos estimados para especies adaptadas al frío podrían infraestimar los límites térmicos superiores y potencialmente exagerar los riesgos del cambio climático. Por otra parte, es improbable que las especies que se encuentran próximas a sus límites térmicos superiores incrementen su tolerancia al calor.

El **Capítulo 2** se enfoca en los lagartos del género *Liolaemus*. Aquí, construyo una filogenia calibrada con el tiempo y analizo los patrones de diversificación del género respecto a la historia cimática y geológica. El origen de la diversificación del grupo se establece más atrás en el tiempo que estimaciones previas, lo que cuestiona la hipótesis de la vicarianza andina como motor de la diversificación. El patrón general de diversificación sugiere la creación gradual de nuevos nichos. Además, se ha detectado que este grupo muestra distintos patrones de diversificación a ambos lados de la cordillera de los Andes, y que la diversificación del grupo argentino (subgénero *Eulaemus*) se relaciona con el cambio de temperatura global.

En el Capítulo 3, incorporo los ragos térmicos fisiológicos a los análisis filogenéticos y estimo la velocidad a la que han ido cambiando en el tiempo. Los resultados muestran que para asimilar el rápido incremento actual de temperatura, los rasgos tendrían que

evolucionar cuatro o cinco órdenes de magnitud más rápido que las tasas más rápidas observadas. Los análisis comparativos filogenéticos muestran que los ragos térmicos de los lagartos del género *Liolaemus* están conservados más allá de los esperado en exclusiva por movimiento Browniano y que las preferencias témicas y las temperaturas medidas en campo muestran más inercia filogenética que los límites térmicos. Todos estos resultados hacen improbable que la adaptación evolutiva de los rasgos térmicos fisiológicos pueda jugar un papel significativo en su respuesta al cambio climático. Además, exploro la posibilidad de emplear métodos compartivos para estimar rasgos que no se han medido en algunas especies a través del grado de parentesco filogenético.

Finalmente en el Capítulo 4 se ha testado la afirmación de que los modelos bioclimáticos deberían ajustarte con variables directas. Utilizo un modelo climático dinámico (*dynamic climate downscaling*) de la península ibérica para calcular temperaturas operativas y usarlas, junto a la temperatura del aire, para crear modelos bioclimáticos de catorce especies de lacértidos. Mis resultados indican que la robustez del modelo es similar cuando se usa temperatura operativa o temperatura del aire y que las tendencias de ambas variables durante la segunda mitad del siglo XX no diferen de forma significativa. Por tanto, mi estudio demuestra que el uso de variables directas no siempre mejora la calidad del modelo.

Introduction

Introducción

Antecedentes y estado actual del tema

EL CLIMA Y LA ACCIÓN HUMANA

Durante la historia de la tierra, el clima ha estado cambiando continuamente debido a procesos geológicos (Raymo and Ruddiman 1992) biológicos (Kopp et al. 2005) e incluso astronómicos (Pope et al. 1997, 1998). Desde el periodo Terciario, el clima global se ha enfriado progresivamente (Zachos et al. 2001) y se han producido importantes fluctuaciones que han provocado episodios glaciales e interglaciales (Hambrey and Harland 1981). Estos cambios han contribuido enormemente a dar forma a los patrones de biodiversidad actuales (Svenning et al. 2015).

Desde la aparición y la dispersión por el mundo del *Homo sapiens* L. gracias a la cultura del fuego (Haber 2007), los humanos también hemos tenido un impacto enorme en los ecosistemas, primero como cazadores-recolectores (e.g., Miller et al. 2005, Sandom et al. 2014) y luego, más profundamente, a través de la agricultura y la ganadería (Haber 2007). Es, sin embargo, a partir de la revolución industrial y con el paso a un sistema productivo basado en el uso de combustibles fósiles – que propicia un espectacular incremento de nuestra población – cuando se multiplica nuestro impacto sobre el planeta, hasta el punto de que se ha propuesto el término 'Antropoceno' para definir la época actual (Steffen et al. 2011). A partir de los años 50 se produce la 'Gran aceleración' en la que los cambios socio-económicos están desembocando en cambios fundamentales en el estado y el funcionamiento del sistema planetario (Steffen et al. 2015). En el comienzo del siglo XXI vivimos en una época en la que las amenazas para la biodiversidad han adquirido una magnitud escalofriante.

CAMBIO CLIMÁTICO Y EVOLUCIÓN

Como apuntaba al principio, los cambios ambientales a gran escala han influenciado enormemente los actuales patrones de diversidad (Svenning et al. 2015). Las cinco grandes extinciones pasadas desde la de la transición Ordovícico-Silúrico hace 450–440 millones de años hasta la del Cretácico-Paleogeno hace 65 millones de años han sido causadas de uno u otro modo por eventos que han influenciado el clima de la tierra, ya sean incrementos masivos de vulcanismo (Campbell et al. 1992), magmatismo (Wignall 2001; Bond and Wignall 2014) o impactos de asteroides (von Frese et al. 2009; Schulte et al. 2010). Sin embargo, el clima ha estado cambiando continuamente y esto no ha conllevado necesariamente extinciones masivas. El efecto de estos cambios depende de que la magnitud y la velocidad a la que tienen lugar permita a las especies adaptarse.

EL CAMBIO CLIMÁTICO ANTROPOGÉNICO Y LOS MÉTODOS DE EVALUACIÓN DE SU EFECTO EN SERES VIVOS

Las emisiones de gases de efecto invernadero producidas por el enorme y creciente uso que se ha ido haciendo de los combustibles fósiles ha provocado que durante el último siglo el clima de la tierra se haya calentando y los patrones están cambiando. En la península ibérica, por ejemplo, encontramos que gran parte incremento de temperatura durante la segunda mitad del siglo veinte se ha centrado en las temperaturas del mes de junio, mientras que este incremento ha sido menor en julio y agosto (ver Apéndice 2). Estos cambios, además, se acentuarán a lo largo de este siglo (IPCC 2013). Además, aunque el clima de la tierra siempre ha sido fluctuante, el cambio climático de origen antropogénico está ocurriendo a una velocidad sin precedentes (IPCC 2013). Es por tanto de capital importancia para la gestión de la biodiversidad ser capaz de predecir los efectos de estos cambios sobre las especies (Thuiller 2007).

Los modelos bioclimáticos constituyen la metodología más utilizada hasta el momento para realizar estas estimaciones (e.g., Araújo et al. 2006). La clave de esta aproximación está en encontrar relaciones estadísticas entre las distribuciones de las especies y el clima. Sin embargo, estos modelos se basan en algunas asunciones ecológicas problemáticas. Asumen, por ejemplo, que la distribución de las especies se encuentra en equilibrio con el ambiente, habiendo evidencia de lo contrario para algunos grupos de especies con baja capacidad dispersiva (Araújo and Pearson 2005). Otra asunción importante es que los nichos ecológicos de las especies no van a cambiar en el tiempo (Wiens et al. 2010).

Incluso sin tener en cuenta estas asunciones, algunos estudios han demostrado que las proyecciones realizadas por distintos modelos pueden ser tan distintas que pueden discrepar en la simple evaluación de si se espera que la distribución de una especie vaya a expandirse o reducirse en un escenario determinado (Pearson et al. 2006; Araújo and New 2007). Para abordar las incertidumbres de estos modelos, los investigadores han propuesto el uso de nuevas técnicas más complejas como el promediado de modelos o la predicción mediante conjuntos de modelos (Araújo and New 2007; Thuiller et al. 2009; García-Valdés et al. 2013). Otra aproximación es el uso de modelos basados en procesos biofísicos (e.g., Kearney and Porter 2004, Kolbe et al. 2010) que analizan mecanísticamente aspectos considerados limitantes del nicho fundamental de las especies. Estos últimos no tienen por qué asumir que la distribución se encuentre en equilibrio con el ambiente, ya que al modelar mecanísticamente procesos subyacentes la causalidad está implícita, por lo que son teóricamente más adecuados para su proyección a nuevas circunstancias (Kearney and Porter 2006). Cabe destacar también la aproximación del herpetólogo y biólogo evolutivo Barry Sinervo que en 2010 realizó un sencillo modelo mecanístico para evaluar el riesgo de extinción en lagartos y fue capaz de aplicarlo a un gran número de especies en varios continentes. El mayor avance de su modelo es que fue capaz de calibrarlo con extinciones reales de lagartos (ver Apéndice 1). No obstante, los modelos mecanísticos sí que asumen que estas relaciones no van a cambiar con el tiempo. Además, el problema de estos modelos es que necesitan gran cantidad de información específica y datos para su correcta calibración y, al existir alrededor de 1,8 millones de especies nominadas y muchas más por documentar, no son prácticos para la pronosticación en estudios de biodiversidad general.

EL NICHO ECOLÓGICO

El primero en acuñar el término 'Nicho' fue Grinnell en 1917, estudiando el nicho del ave *Toxostoma redivivum* y con el se refería a los requerimientos climáticos y de hábitat (i.e., los factores ambientales) expresados geográficamente que permitían su presencia. Diez años después, Elton (1927) interpretó el nicho como el rol fundamental de la especie en la comunidad. Estas dos visiones (nicho grinneliano y nicho eltoniano) han perdurado hasta la actualidad. Más adelante, Hutchinson (1957) definió el nicho como un hipervolumen de variables ambientales "cada punto del cual corresponde con un estado del ambiente que permite a la especie existir indefinidamente". Esta definición se acerca mucho más al concepto grinneliano del nicho. Algo más tarde, Hutchinson (1978) diferenció los tipos de variables que definen el nicho en scenopoéticas, que no son consumidas y por las que no hay competencia y bionómicas, que son consumidas y pueden ser objeto de competición. La diferenciación entre unas variables y otras depende de la especie que tratemos, la vegetación, por ejemplo, puede ser una variable bionómica para un hervíboro, pero una variable scenopoética para un insectívoro pequeño. Sin embargo, ejemplos claros de variables generalmente scenopoéticas son las variables climáticas y geomorfológicas (Peterson et al. 2011). En esta tesis trabajamos con el concepto grinneliano del nicho y tratamos la temperatura como una variable scenopoética.

Una última distinción se hace entre el nicho fundamental (i.e., todos los estados ambientales que pueden permitir la existencia de la especie 'X') y el nicho realizado (i.e., la parte del nicho fundamental que corresponde con las condiciones ambientales en las que la especie 'X' es un buen competidor y puede persistir) (Hutchinson 1957).

CONSERVATISMO DE NICHO

La relación entre la similitud ecología/biológica y el parentesco evolutivo entre especies se denomina 'señal filogenética'; cuando las características ecológicas ancestrales se mantienen más allá de lo esperable simplemente por el parentesco evolutivo se considera 'conservatismo filogenético'; si están conservadas las características que definen el nicho ecológico, hablamos de 'conservatismo de nicho' (Losos 2008). Este es hoy en día un concepto sujeto a controversia (Crisp et al. 2009 y referencias en el texto), pero sigue siendo importante para ayudar a explicar fenómenos de especiación alopátrica, biogeografia histórica y patrones de riqueza de especies (Wiens and Graham 2005). Normalmente se asume que hay algún grado de conservatismo en el nicho fundamental (ver Peterson et al. 2011 para una revisión del concepto de nicho), lo que permite cierta predictabilidad a través de los taxones, dimensiones ambientales y marcos temporales cuando las respuestas a las variables abióticas se investigan desde una perspectiva evolutiva (e.g. Jablonski et al. 2006, Romdal et al. 2013).

Justificación y objetivos de la tesis

¿PUEDE EVOLUCIONAR EL NICHO ECOLÓGICO?

Como se ha visto a lo largo de la introducción, existen ejemplos de caracteres que están más conservados que otros (e.g., Addo-Bediako et al. 2001, Kellermann et al. 2012a, b), y hay ejemplos tanto de cambios rápidos de nicho (Johnston and Selander 1964; Phillips et al. 2006; Buswell et al. 2011) como de lo contrario. (Kozak and Wiens 2010; Bystriakova et al. 2011). Por lo tanto no está completamente claro que la asunción de conservatismo de nicho para la proyección de las distribuciones de especies a nuevas circunstancias sea válida en general. Dependiendo de la tasa a la que el nicho de una especie pueda cambiar, las predicciones del efecto del cambio climático sobre la especie basadas en modelos de nicho ecológico pueden estar sobreestimando el cambio en el rango de distribución potencial de las especies. Esto puede llevar a una política de conservación errónea en especies supuestamente amenazadas por el cambio climático.

PRESENTACIÓN Y OBJETIVOS

En la presente tesis doctoral se abordan estas cuestiones desde una perspectiva macrofisiológica, ecofisiológica y evolutiva. En particular, me he enfocado en algunos de los caracteres ecofisiológicos que definen la relación entre los organismos y la temperatura. Para ello se ha realizado un estudio ecofisiológico a gran escala en Chile, utilizando como principal modelo de estudio el género de lagartos iguánidos *Liolaemus*. Este grupo y área de estudio se escogieron por varias razones. Por un lado, Chile cuenta con un gradiente climático muy amplio, y por otro *Liolaemus* es uno de los géneros más diversos dentro de los reptiles (Labra et al. 2009), solo superado por *Anolis*. Además, la dependencia de los ectotermos de fuentes de calor externas para regular su temperatura corporal y, por tanto, su fisiología los hacen un grupo muy apropiado para el estudio del efecto del clima en los organismos.

OBJETIVO GENERAL Determinar hasta qué punto está conservada la ecofisiología térmica y evaluar la capacidad de adaptación de los lagartos *Liolaemus* al aumento de temperatura.

MAIN OBJECTIVE To determine how conserved is thermal physiology in relation to temperature and evaluate how plausible is for *Liolaemus* lizards to adapt to increasing temperatures.

OBJETIVOS ESPECÍFICOS

1 | Evaluar cuan conservada está la relación entre la fisiología y la temperatura en organismos terrestres. (Capítulo 1)

2 | Analizar el patrón de diversificación de los lagartos del género *Liolaemus* en relación con la historia climática y geológica. (Capítulo 2)

3 | Estudiar la relación entre la fisiología térmica y la filogenia. (Capítulo 3)

4 | Estimar la velocidad de evolución de estos caracteres ecofisiológicos y evaluar la posibilidad de que evolucionen en un contexto de calentamiento global. (Capítulo 3)

5 | Estudiar cómo se pueden utilizar los métodos comparativos para mejorar los modelos de nicho, usando la filogenia para estimar caracteres ecofisiológicos en especies no estudiadas. (Capítulo 3)

6 | Evaluar cómo ha cambiado el ambiente térmico durante los últimos 60 años, el periodo en el que el cambio climático ha sido más intenso. (Capítulo 4)

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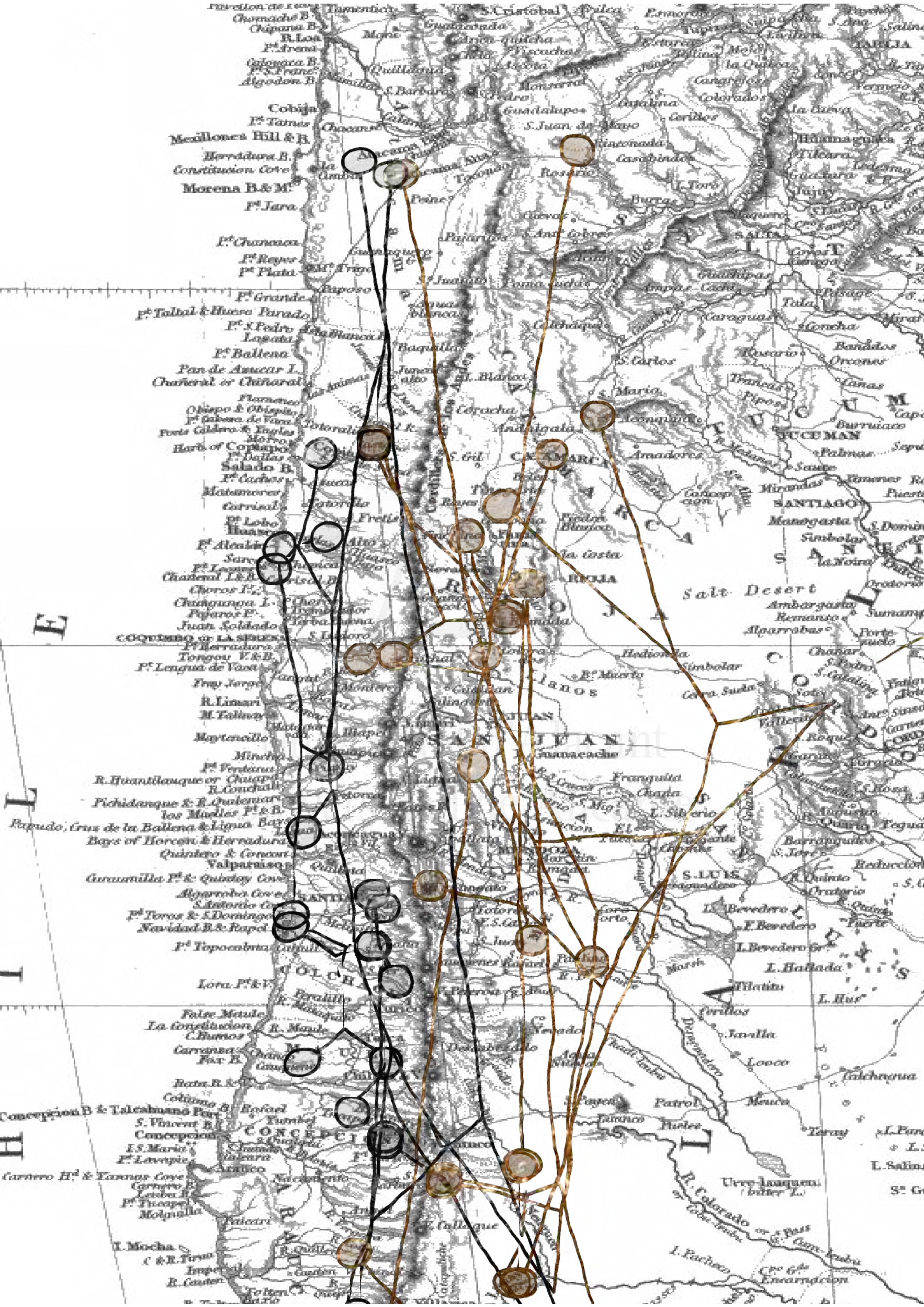
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Herradura B.
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Morena B. & Mt.
Pt. Jara
Pt. Chanaral
Pt. Reyes
Pt. Plata
Pt. Grande
Pt. Taltal & Huesa Parado
Pt. S. Pedro
Lagata
Pt. Ballena
Pan de Azucar I.
Chañeral or Chañaral
Flamenco
Obispo & Obispito
Harb. of Copiapo
Salado B.
Pt. Caldera
Matamoros
Carrizal
Pt. Lobo
Huasco
Pt. Alcalde
Sarco
Chañeral I.
Choros Pt.
Chungunga I.
Pajaros Pt.
Juan Soldado
COQUIMBO or LA SERENA
Pt. Herradura
Tongoy
Pt. Lengua de Vaca
Fray Jorge
R. Limari
M. Talinay
Maytencillo
Mincha
Pt. Verdana
R. Huantilauque or Chuapa
R. Conchali
Pichidanque & E. Quelemar
los Molles
Papudo, Cruz de la Ballena & Ligua Bay
Bays of Horcon & Herradura
Quintero & Concon
Valparaiso
Curaumilla Pt. & Quisley Cove
Algarroba Cove
S. Antonio Cove
Pt. Toros & S. Domingo
Navidad B. & Rapel
Pt. Topocalma
COLCHAGUA
Lora Pt.
False Maule
La Constitucion
R. Maule
Carranza
Fox B.
Rata B.
Colomo
Concepcion B. & Talcahuano
S. Vincent B.
Concepcion
I. S. Maria
Pt. Lavapie
Arauco
Carnero Hd. & Xarnas Cove
Molguilla
I. Mocha
Imperial
R. Cauten
CONCEPCION
S. Cristobal
Atacama
Calama
Chacance
Guadalupe
S. Juan de Mayo
Rinconada
Casabindo
Rosario
Toconao
Humahuaca
Tilcara
SALTA
Jujuy
Catalina
TARIJA
Pajaros
Paposo
S. Carlos
Rosario
Concha
Bandidos
Orcones
Tinogasta
Catamarca
Andalgala
Aconquija
TUCUMAN
Amadores
Santiago
Manogasta
Simbolar
Salt Desert
RIOJA
Famatina
Hediondas
Llanos
S. Pedro
S. Catalina
Cordova
SAN JUAN
Guanacache
S. LUIS
Mendoza
Chacabuco
L. Bevedero
L. Hallada
R. Quinto
Tilatilu
Sa. Rosa
Reduccion
Loncomilla
Yavilla
Loco
Calchugua
Patroi
Pulga
Taraj
Urre-lauquen (bitter L.)
R. Colorado
I. Pacheco
Encarnacion
CHILE
LA PAMPA
Descabezado
Tucuman

Chapter I

Capítulo I

Los resultados de este capítulo han sido publicados en:

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*Ambos autores contribuyero de forma similar.

Heat freezes niche evolution

INTRODUCTION

There is a general expectation that climate, both at present and historically, governs the broadest outlines of species distributions. The degree to which climatic preferences of species and climatic tolerances are conserved across lineages is still a matter of debate, as rates of niche evolution and the mechanisms underlying them remain poorly known (e.g., Losos 2008). The assumption is that some significant degree of conservatism exists of the fundamental niche—the set of environmental states that permits species to persist (sensu Hutchinson 1957; for recent review of niche concepts see also Peterson et al. 2011)—which provides predictability across taxa, environmental dimensions, and time frames, when species responses to abiotic variables are investigated from evolutionary and ecological perspectives (e.g., Jablonski et al. 2006; Romdal et al. 2013). Nonetheless, a growing number of analyses suggest that key traits affecting physiological tolerances, which contribute to setting the fundamental niche, show much variation in the extent of their conservatism. Compelling examples include little systematic environmental variation in the sum of effective temperatures for insect development, compared with much rainfall-related variation in desiccation resistance for the same group (e.g., Addo-Bediako et al. 2001), and, in *Drosophila*, differences among various traits in the scope of their variation (e.g., Kellermann et al. 2012a; Kellermann et al. 2012b).

In keeping with the finding that some traits show much variation, adaptations to recent climate change have been reported in several taxa, mostly involving phenological adaptation to shifts in the timing of seasonal events (e.g., Visser 2008), but also involving changes in the geographic distribution of genetic polymorphisms (e.g., Umina et al. 2005). Recorded differences among climatic niches in the native and non-native ranges of invasive species have also led to the suggestion that niches might have evolved during the invasion process (e.g., Broennimann et al. 2007; Fitzpatrick et al. 2007). Notwithstanding, tests of niche conservatism (sensu Losos 2008; i.e., whether niches change more slowly than expected from Brownian motion evolution) with measures of overlap between climatic niches inferred using methods that relate geographical distributions of species to aspects of climate have one important limitation: the theoretical expectation of conservatism is justified for fundamental (abiotic) niches rather than for realized niches (Araújo and Peterson 2012).

Realized niches are a subset of the fundamental niche reduced by the effects of dispersal, biotic interactions, and, with animals, by aspects of behaviour that affect resource utilization (e.g., Peterson et al. 2011). Although these factors are constrained by traits that, themselves, are expected to be conserved over long periods of time, the realized niches emerging from interactions between traits and the environment are not expected to be conserved. For example non-physiological mechanisms of adaptation, such as thermoregulatory behaviour used by ectotherms to regulate physiological performance (and allow survival beyond species thermal tolerance limits), are often labile. Simulations have shown that such behavioural adaptations can even constrain rather than drive evolution (Huey et al. 2003), thereby reinforcing conservatism of the fundamental niches; an outcome being borne out by empirical work (e.g., Marais and Chown 2008). Another extreme case of lability in factors influencing realized niches are changes in diet. Adélie penguins in Antarctica, for example, were able to switch in <200 yr from a diet mainly composed of fish to one predominantly based on krill (Emslie and Patterson 2007). Although several of the factors determining realized niches of species are unlikely to remain stable through time, tests of conservatism are typically based on measurements of the realized niche (e.g., Hof et al. 2010; Kozak and Wiens 2010). It follows that, since realized niches generally represent subsets of the fundamental niche, and ecological conditions in different times or regions can lead to different occupation of the fundamental niche (e.g., Jackson and Overpeck 2000), shifts in realized niches are often likely to indicate that different portions of the fundamental niche are being occupied rather than that evolutionary changes in the fundamental niche have taken place.

The significant question thus remains of whether physiological adaptation to ongoing climate warming or conservatism of climatic tolerances is more likely. Answers to this question are important for several reasons. First, several studies have suggested that a suite of tropical to sub-tropical ectotherms may be close to their thermal safety margins, which, if exceeded, could lead to the extinction of several species (Deutsch et al. 2008; Huey et al. 2009; Clusella-Trullas et al. 2011). Population-level assessments of reptiles suggest that climate-change driven extinctions may already be occurring (Sinervo et al. 2010), while some studies suggest that tropical endotherms may be similarly at risk (Cooper et al. 2011). Meta-analysis for many different terrestrial organisms are also showing that distributions of species have recently shifted to higher elevations at a rate of 11 meters per decade, and to higher latitudes at a rate of 16.9 km per decade, thus compromising the ability of several species to adapt to ongoing climate change by tracking shifting climate suitability (Chen et al. 2011). Second, understanding the scope for niche evolution is critical because the assumption of little evolutionary change underlies many projections of climate change effects on species distributions, both in the past (e.g., Nogués-Bravo et al. 2008) and future (e.g., Garcia et al. 2012). Third, the extent to which niche evolution takes place is a fundamental question in biogeography and evolution, with strong implications for understanding the origin, diversification and distribution of life on earth, and fundamental differences therein between marine and terrestrial systems (e.g., Wiens and Donoghue 2004; Sunday et al. 2012; Romdal et al. 2013).

Is evolution of climatic niches asymmetric?

Questions regarding the evolution of the fundamental niches are difficult to address for at least three reasons. First, measuring the fundamental niche of a species is challenging because the full set of dimensions that constitute a species' niche is unknown and is likely to vary from one species to another. Furthermore, interactions between dimensions of the niche, e.g., temperature and water, can modify the tolerance of species to individual niche dimensions in ways that are not always easily predicted (e.g., Crimmins et al. 2011). Second, experiments measuring aspects of the fundamental niche are expensive and time consuming thus being typically limited to small numbers of species. Third, demonstrating changes in one aspect of the niche of a species might provide little information about potential evolutionary changes in other aspects thereof (e.g., Angilletta et al. 2003). Nonetheless, biophysical approaches are demonstrating that a limited suite of traits can readily characterize important aspects of the fundamental niche, and that many of these have to do with thermal biology (Porter and Kearney 2009; Kearney et al. 2010). Indeed, suggestions have recently been made that the stage on which ecological and evolutionary interactions play out should be termed the 'thermodynamic niche' (Kearney et al. 2012). In consequence, investigations of differential variation in traits underpinning thermal biology are likely to provide important insights into the extent to which fundamental niches might evolve, and what the consequences thereof are for species distribution modelling and for predicting species responses to climate change, especially in environments as different as those found in marine and terrestrial systems (e.g., Sunday et al. 2012).

For many terrestrial animals and plants the upper and lower thermal limits to performance are significant components of the thermal niche (e.g., Larcher 1995; Pörtner 2001; Hoffmann 2010). Specifically, for a number of terrestrial animal ectotherms, it has been shown that upper and lower thermal tolerance limits covary to only a limited extent or do not do so at all (Addo-Bediako et al. 2000; Hoffmann et al. 2013). However, in others, stronger covariation exists (e.g., Calosi et al. 2010). In marine groups such covariation is especially pronounced, perhaps owing to oxygen limitation of thermal tolerance (Pörtner 2010; Sunday et al. 2011). In consequence, whilst evidence of general patterns is emerging for ectotherm animals (e.g., Addo-Bediako et al. 2000; Sunday et al. 2011; Kellermann et al. 2012b; Grigg and Buckley 2013; Hoffmann et al. 2013), how extensive the asymmetry in variability of upper and lower tolerances is among terrestrial organisms, and what its implications are for niche evolution in particular have not been comprehensively explored across a wide range of terrestrial plants and animals.

VARIATION IN CRITICAL THERMAL LIMITS ACROSS TAXA

Here, we explore the extent of the asymmetry in upper and lower tolerances by examining standardized metrics of thermal tolerance for 3080 terrestrial ectotherm, endotherm, and plant species with data spanning distributions across the world (Figure 1; for full description of the data see Tables S1-S5 and references provided in the supporting online material section). Because thermal tolerance metrics are not fully comparable across studies (both within and between biological groupings), data were subdivided and analyzed separately for each metric.

For ectotherms a first group (A) included critical minimum temperatures (CT_{min}) and critical maximum temperatures (CT_{max}) matched for 129 reptiles, minimum lethal temperatures (LT_{min}) and CT_{max} matched for 26 amphibians, and CT_{min} and CT_{max} matched for 12 spiders and 40 insects (Sunday et al. 2011; Hoffmann et al. 2013). The second group (B) includes estimates of CT_{min} and CT_{max} matched for 38 insect species (from Deutsch et al.

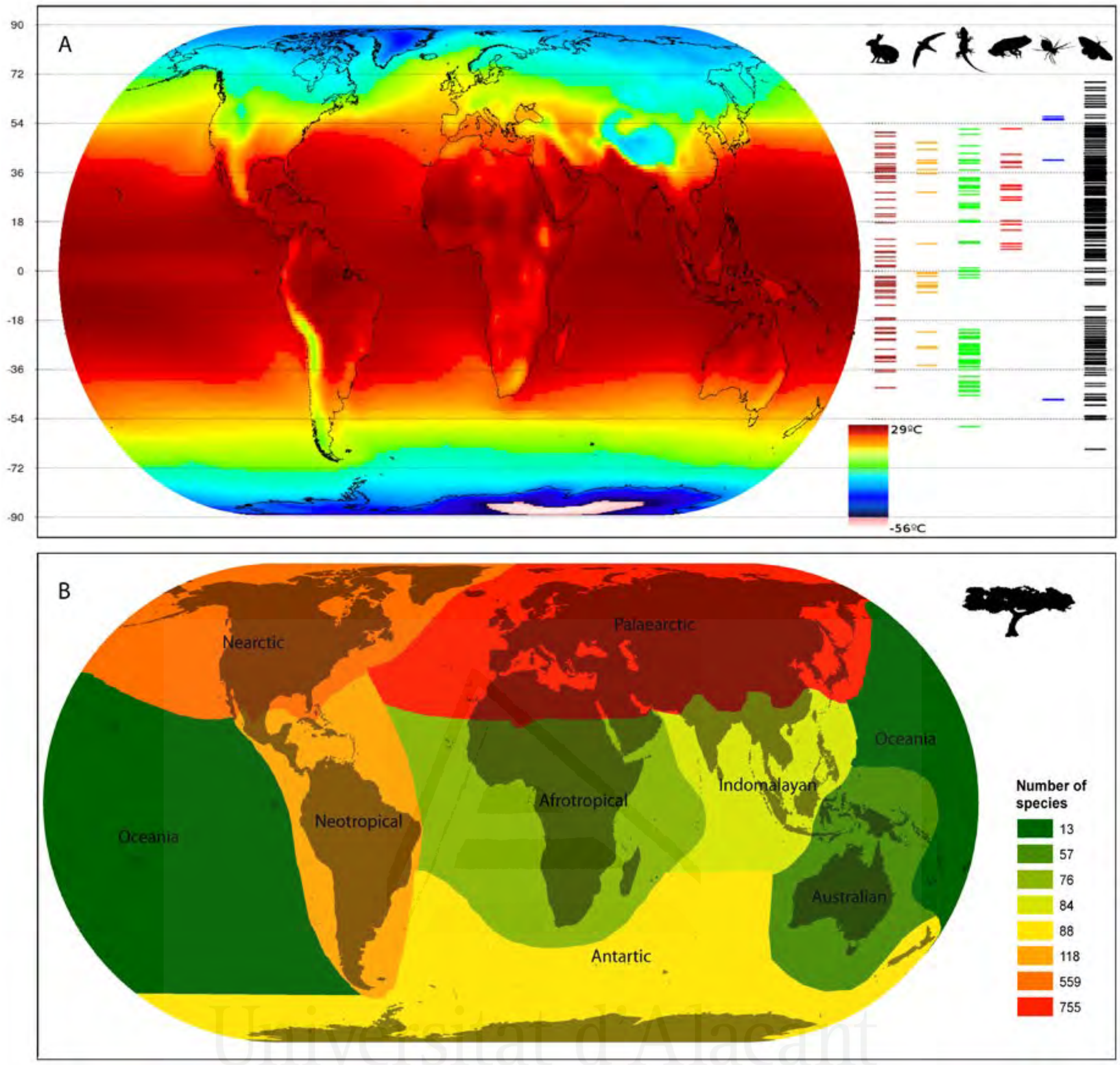

Figure 1. Distribution of the thermal tolerance data utilized in this study. (A) Colors depict annual mean temperature and bars on the right represent the centroids of species ranges calculated with data provided by Holt et al. (2013). Black bars are centroids of the range of insect species, spiders are represented with blue bards, amphibians are represented with red bars, reptiles are represented with green bars, birds are represented with orange bars, and mammals are represented with brown bars. (B) Udvardy's plant Biogeographical Provinces of the World. Since maps of distributions of the plant species were not available for us, we grouped assigned species to their native realms so that colors represent the number of species with thermal data per realm.

2008). Notice that the latter metrics are estimated from performance curves of the rate of development of organisms at different temperatures, so they are not directly comparable with other critical thermal measurements. The third group (C) includes a mix of metrics (CT_{min} and CT_{max}, lethal maximum and minimum temperatures in which 50% of the individuals die (LT_{min50} and LT_{max50}), and lethal maximum and minimum temperatures in which 100% die (LT_{min100} and LT_{max100}) for 704 insects (Kellermann et al. 2012b; Hoffmann et al. 2013). While the data sets A and B include upper and lower tolerances matched for each individual species, the third data set includes unmatched upper and lower thermal tolerances across species. These unmatched data provide a less powerful comparison, but due to the substantial sample size we elected to analyze them, while distinguishing these data from those where lower and upper tolerance metrics were matched for every species.

For endotherms we reviewed eighty-four studies determining Thermal Neutral Zone (TNZ) boundaries for birds and mammals, i.e., the range of external ambient temperatures in which the resting metabolic rate is constant and minimum (McNab 2012), and constructed a database of paired Lower Critical Temperatures (L_{CT}) and Upper Critical Temperatures (U_{CT}) for 166 species (see supporting online material).

For plants we reviewed thirty-five physiological studies using photosystem II (PSII), a protein complex that is related with the performance and survival of plants under extreme temperatures (e.g., Valladares & Pearcy 1997). Non-destructive measurements of chlorophyll fluorescence determining the maximal efficiency of PSII photochemistry (*F*v/*F*m) of the leaves are recorded as temperatures are increased or decreased under controlled laboratory conditions (e.g., Gimeno et al. 2009). The critical temperature promoting a reduction of 50% of the initial *F*v/*F*m values (LT_{50}) was then obtained after fitting the corresponding response curves. This metric has been shown to correlate with other physiological estimates of thermal tolerance, such as membrane breakage and electrolyte leakage (Sierra-Almeida & Cavieres 2010) (Sierra-Almeida and Cavieres 2010), although lower performance limits may be set more by constraints on growth than on photosynthesis, at least for elevation tree lines (e.g., Hoch and Körner 2012). When data on LT_{50} was not provided in the papers reviewed, whenever possible, we estimated it from alternative measures such as *T*c, the critical temperature, defined as the intersection of the lines extrapolated from the slow and fast rise portion of the temperature basal fluorescence response curve, which is highly correlated with LT_{50} (e.g., Zhang et al. 2012). Regression lines obtained from studies simultaneously reporting various parameters were used to estimate LT_{50} values from studies only providing values for these alternative parameters. Overall, LT_{50} values were obtained for 520 plant species, 64% of them for cold tolerance, 36% for heat tolerance, with paired data representing only 4% of the total ($n=19$). Estimates of cold tolerance were also available for a large number of plant species, specifically cold hardiness ($n=1190$) and frost tolerance ($n=106$), but no analogue measurements were found for heat tolerance which is expressed as number of days above 30ºC that the species is able to tolerate but not as absolute temperature; thus results regarding these measures are provided in the supporting information section.

Regarding ectotherms, more specifically reptile species from group A, we found that CT_{max} averaged 42.2 ºC with variance 8.2, whereas CT_{min} was 7.8 ºC with variance of 13.0 (Figure 2A). Similar differences between CT_{max} and LT_{min} were found for amphibians, with two-fold increases in the variance of tolerance to heat versus cold (11.3 vs. 20.7), and for spiders with 6-fold increases of variance (2.6 vs. 16.7) (Figure 2A). For insects, we recorded almost 2-fold increases of variance (29.0 vs. 41.1) with data from group A (Figure 2A), and roughly the same with group B (13.8 vs. 30.6) (Figure 2B). With the unmatched lower and upper tolerance values with data from group C (Figure 2C) the same general

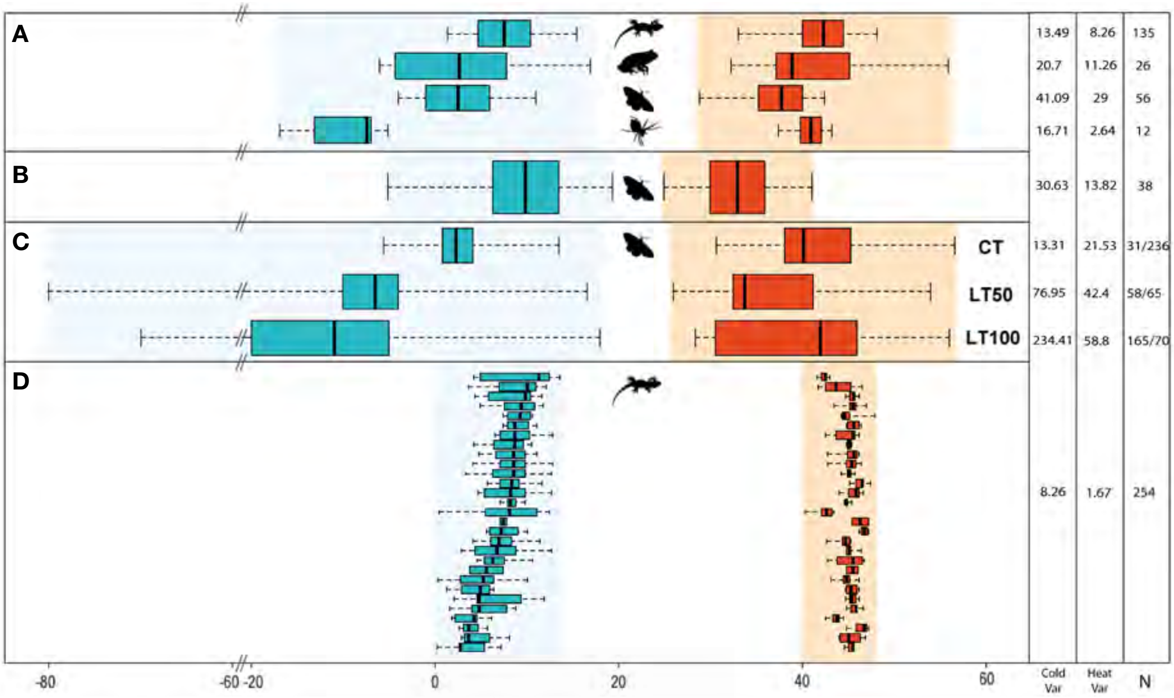

Figure 2. Variance of cold tolerance (green plots, left) versus heat tolerance (red plots, right) among terrestrial ectotherms. (A) Box plots of CT_{min} and CT_{max} for 129 species of reptiles and LT_{min} and CT_{max} for 26 species of amphibians, and CT_{min} and CT_{max} for 12 spiders and 40 insects (Sunday et al. 2011; Hoffmann et al. 2013); (B) Box plots of CT_{min} and CT_{max} for 38 species of insects (data from Deutsch et al. 2008); (C) Box plots of a mix of unmatched lower and upper CT and LT values for 704 insects (Kellermann et al. 2012b; Hoffmann et al. 2013); (D) Box plots of CT_{min} and CT_{max} for 29 *Liolaemus* lizard species (each one of the 29 boxes represents intraspecific variation among individuals of the same species) in Chile (FFY unpublished).

pattern emerged (variance of lower tolerance=142.2 with N=352, and variance of upper tolerance=37.9 with N=403), with lethal minimum temperature values extending far below any CT_{min} measurement for ectotherms (Figures 2A and 2B) and below LT_{min} values reported for amphibians (Figure 2A).

To explore the prediction that intraspecific niche variation is also lower near the critical thermal maximum than near the thermal critical minimum, we analyzed data from 29 species of South American *Liolaemus* lizards from Chile for which several individual replicates exist for different species (mean number of individuals per species 9 ± 4.2, unpublished data from FFY, see details on the method for data collection the in supplementary material). Results of intraspecific variation of thermal niche traits for the Chilean lizards were consistent with interspecific variability found among other ectotherms, i.e., lower for intraspecific CT_{max} than for CT_{min} (Figure 2D). Critical maximum temperatures (CT_{max}) among Liolaemus species averaged 45.0 °C (Variance=1.7) and critical minimum temperatures (CT_{min}) averaged 7.4 °C (Variance = 8.3) (Figure 2D).

The same pattern of asymmetrical variation in lower and upper thermal tolerances for ectotherms was recorded for endotherms and plants. Mean LCT (Lower Critical Temperatures)

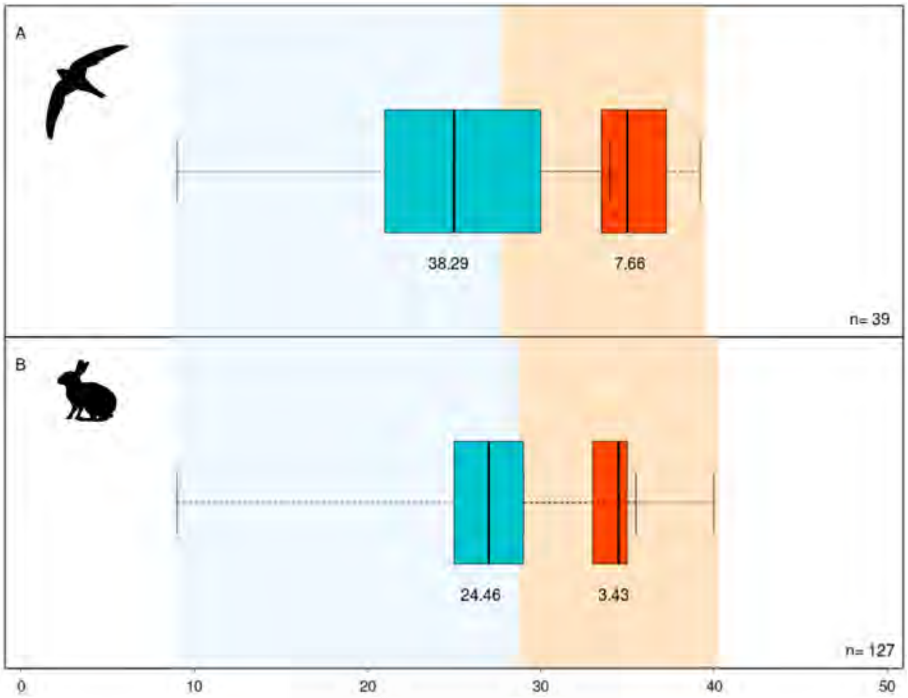

Figure 3. Variance of cold tolerance (green plots, left) versus heat tolerance (red plots, right) for endotherms. Variances are depicted below every boxplot, number of species (*n*) is on the lower right section of the graph.

and UCT (Upper Critical temperatures) for birds were 24.6 °C and 35.1 °C, respectively, with estimates of cold tolerance being more than four times as variable as heat tolerance (Figure 3A). For mammals, average LCT and UCT were 26.5° C and 34.2 °C, respectively, and variances of L_{CT} were more than seven times larger than variances of U_{CT} (Figure 3B).

For plants the differences in variance were even more striking. For the subset of species with paired measurements of cold and heat tolerance (Figure 4A), mean critical values were -20 °C and 46 °C for cold versus heat tolerance and variances were almost 24 times greater for cold tolerance than for heat tolerance. For the species with unpaired measurements, mean critical values were -12 °C and 47 °C, and variances were five times greater for critical tolerances to cold than to heat (Figure 4B). Even greater variances existed for measurement of frost tolerance and cold hardiness (Figure S2), but no analogue metrics were available for upper limits.

VARIATION IN CRITICAL THERMAL LIMITS ACROSS ENVIRONMENTAL GRADIENTS

Given the asymmetry in variation of lower and upper thermal limits found in previous analyses (e.g., Addo-Bediako et al. 2000), and stronger relationships between lower limits and latitude than between upper limits and latitude (e.g., Sunday et al. 2011), we expected that a positive correlation should exist between lower thermal limits and ambient temperature. Likewise, a much weaker relationship should be expected for upper thermal limits and ambient temperature. In other words, if tolerances to low temperatures are

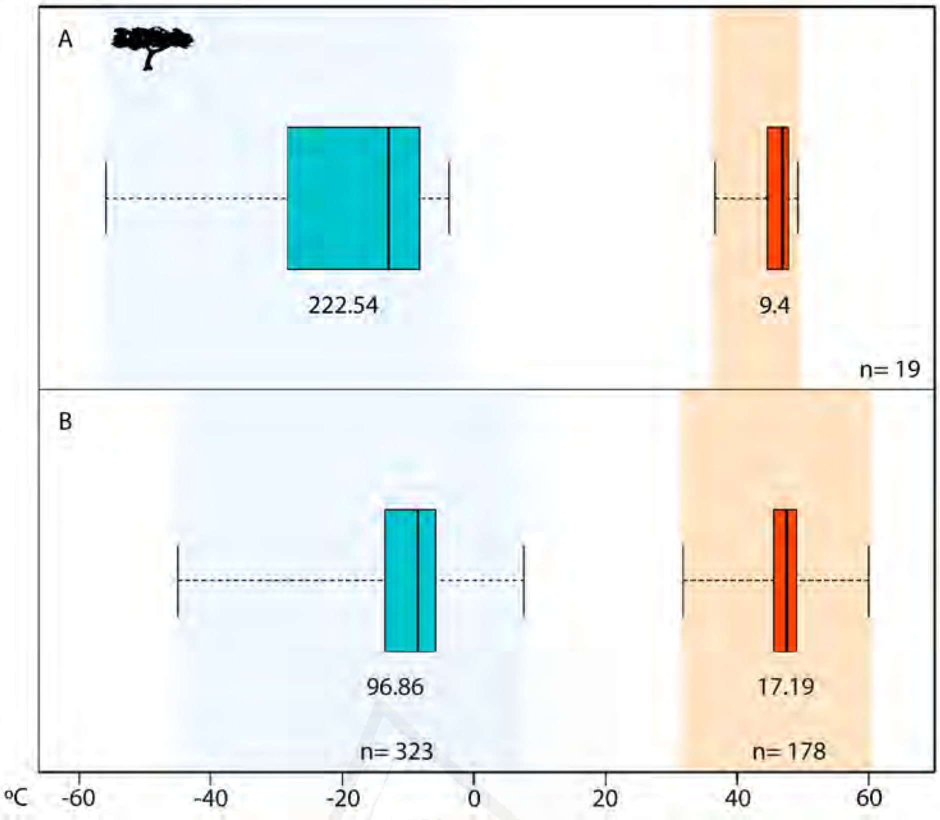

Figure 4. Variance of cold tolerance (green plots, left) versus heat tolerance (red plots, right) among terrestrial plants. Physiological estimates of plant cold tolerance and heat tolerance (LT_{50}) are provided for (A) paired data and (B) unpaired data.

highly labile and lability is driven by natural selection, species exposed to low temperatures should have a tendency for greater tolerance to cold while species not exposed to low temperatures should have a tendency for reduced tolerance to cold. In contrast, if tolerances to high temperatures are highly conserved across clades, natural selection might not be expected to be acting strongly on this trait, resulting in a weak relationship. We examined these expectations by plotting physiological metrics of critical tolerance (CT_{max} and CT_{min} for ectotherms and UCT and LCT for endotherms) against metrics of ambient temperature averaged across species ranges. Notice that plotting biological patterns against environmental gradients is generally preferable than plotting them against geographical clines (such as latitude or altitude), as the latter are usually only indirectly related to the patterns of interest (see for discussion Hawkins and Diniz-Filho 2004; Korner 2007). We also compensated for the allometric relation between LCT and mass (McNab 2012), by fitting a linear model of LCT with the log-transformed body weight in mass and using the residuals to assess the relationship with ambient temperatures.

The chosen ambient temperature metrics are commonly used in modelling studies of species distributions (e.g., Peterson et al. 2011) and include: minimum temperature of the coldest month (T_{min}), maximum temperature of the warmest month (T_{max}), and mean annual temperatures (T_{mean}). The analysis comparing upper and lower thermal limits against ambient temperatures was only possible for a subset of the species in our database with

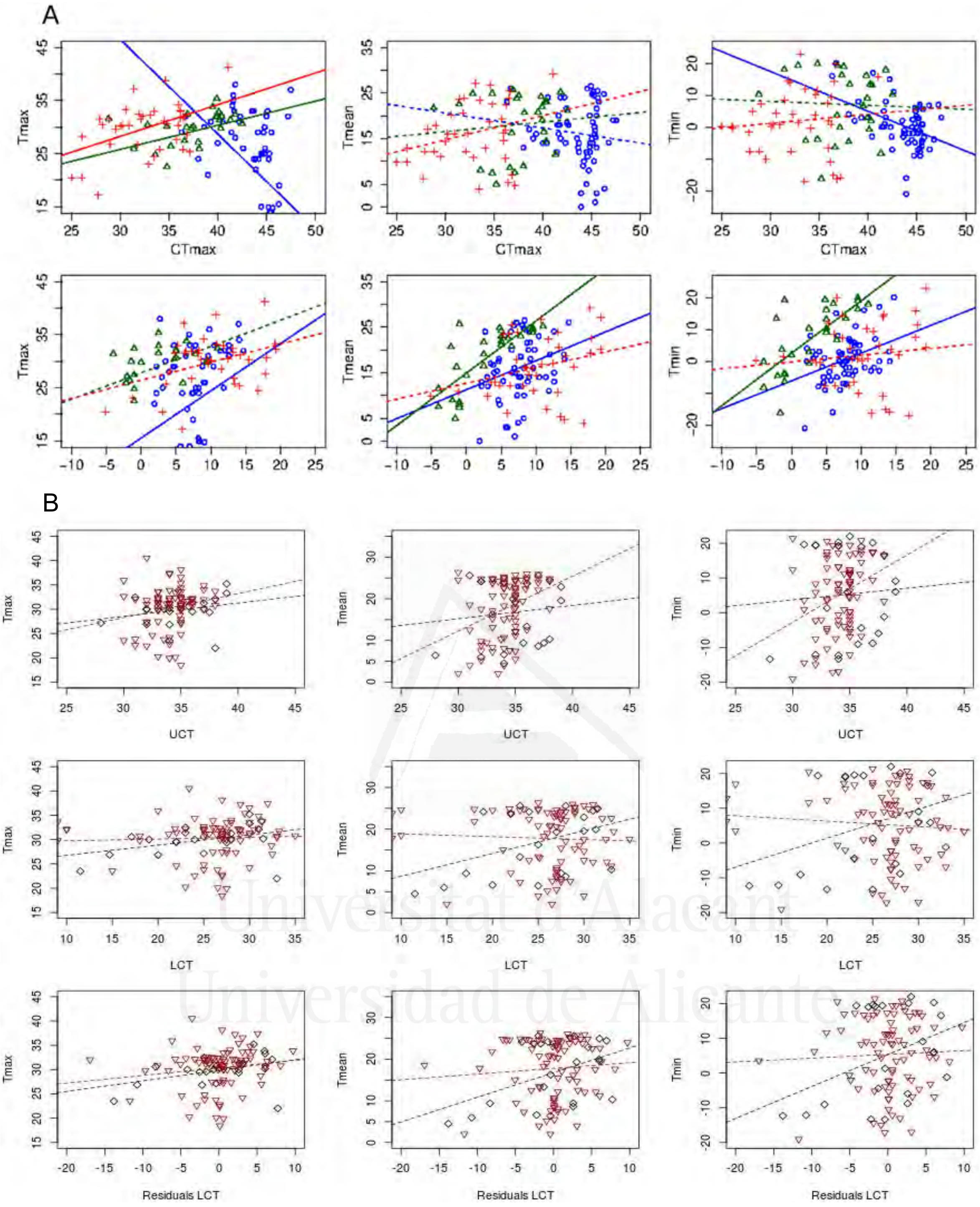

Figure 5. Scatter plots and regression lines between thermal tolerances and ambient temperatures for A: 64 species of reptiles (Blue circles), 26 species of amphibians (green triangles), 38 species of insects (from Deustch et al 2008; red crosses) and B: 22 species of Birds (black squares) and 75 species of mammals (brown inverse triangles). Tmean: yearly mean temperature, Tmax: Maximum temperature of warmest month and Tmin: minimum temperature of coldest month (Data from Hijmans et al. 2005). CT_{max}: Critical Thermal Maximum, CT_{min}: Critical Thermal Minimum (Lethal Thermal minimum for amphibians), UTC: Upper Critical Temperature for endotherms, LTC: Lower Critical Temperature for endotherms. There is an allometric relation between cold tolerance and body mass in endotherms that can mask the relationship between climate and cold to-

lerance. To account for this relation we plot the residuals of a model between body mass and LTC for endotherms (Residuals LTC). Distribution data for reptiles has been downloaded from www.iucnredlist.org, distribution data for amphibians, mammals and birds has been used from Holt et al. (2012), geographical data for insects consists in point locations where experiments with the species were conducted. Values of environmental temperature are calculated as averages across the distribution of the species for reptiles, amphibians and endotherms while the environmental values in the geographic coordinates provided by Deustch et al. (2008) was used for insects.

both physiological data and geographical distributional data, i.e., 64 reptiles, 24 amphibians, 38 insects, 22 birds, and 79 mammals.

As expected, for ectotherms, we found that positive correlations exist between CT_{min} and averaged ambient temperatures (Figure 5A, for correlations and *P*-values see Table S5). Although the strength of the correlations varies with taxonomic groups, the relationship is positive for all. In contrast and consistent with our expectations, we found no clear pattern of correlation between CT_{max} and ambient temperatures (Figure 5A). For example, for reptiles the correlation between CT_{max} and metrics of ambient temperature is markedly negative leading to the suggestion that adaptation to heat among these species might be driven by more complex relationships with a variety of climate variables (see discussion in Clusella-Trullas et al. 2011; Grigg and Buckley 2013). Indeed, most species have similar tolerances to heat (42 °C) and this is independent of the environments they are exposed to (e.g., *Zootoca vivipara* is exposed to T_{min} across the range of -20 °C and the species has as CT_{max} of 43.9 °C, whereas *Sphaerodactylus klauberi* is exposed to T_{min} of 16 °C and has CT_{max} of 36.3 °C). For amphibians, the correlation is either close to zero (with T_{mean}), clearly positive (for T_{max}), or slightly negative (for T_{mean}). For insects the correlation is positive but weak for all three metrics (i.e., always below $\rho = 0.35$).

For endotherms, there is an apparent lack of correlation between thermal limits and ambient temperature for birds (Figure 5B, for correlations and *P*-values see Table S6). A weak positive correlation was found for U_{CT} and mean and minimum temperature in mammals ($\rho = 0.304$, $\rho = 0.302$ respectively). For birds, T_{max} correlates with residuals of cold tolerance ($\rho = 0.422$). In other words, we found partial support for the prediction that natural selection might be driving physiological responses of mammals and birds to changes in ambient temperature (evidence for birds is restricted to T_{max}). In contrast, limited evidence supports the physiological adaptation to heat is constrained by the environment with the exception of T_{max} for which a weak signal of adaptation was detected.

The most prominent feature of the above analysis is that, as expected, CT_{min} and LCT tend to have a positive relationship with ambient temperature. By and large, ectotherm and endotherm species living in cold environments tend to be more tolerant to cold than ectotherm and endotherm species living in warm environments. In fact, TNZ is wider for rodents that evolved in cold climates than of those from warm climates (see Appendix 4). Also, as predicted, species with greater tolerances to heat are not necessarily restricted to warmer environments. Correlations of CT_{max} and UCT with ambient temperature were either close to zero, weakly positive, or negative. Nonetheless, a consistent tendency for increased positive correlation between upper thermal limits among ectotherms (except for reptiles) and endotherms and T_{max} was detected. This is because some of the species with greater tolerances to high temperatures do live in the warmest environments (but species with great tolerances to heat are also found in colder zones). If such tendency were to be broadly confirmed it should indicate that some degree of selection, even if weak, might be occurring for upper thermal limits in warmer environments (but always below 50 ºC, see following discussion on 'hard' physiological limits). Further exploration of this idea, and the general tendencies we have confirmed here building on previous work (Addo-Bediako et al. 2000; Clusella-Trullas et al. 2011; Sunday et al. 2011), are clearly required, especially taking more explicit account of phylogenetic correlation. Although we did not do so here, for reasons of disparate taxa and lack of phylogenies covering them, our findings are consistent with those of previous investigations which have used a variety of approaches, and all of which have resulted in similar findings (e.g., Sunday et al. 2011, 2012; Hoffmann et al. 2013).

WHY WOULD EVOLUTION OF CLIMATIC NICHES BE ASYMMETRIC?

Our synthetic overview and further analyses unequivocally show that variation in thermal tolerances among terrestrial organisms is asymmetric (for syntheses of results see also Figure S1). Specifically, a remarkable contrast of variability exists between interspecific tolerances to cold versus heat among a large sample of terrestrial ectotherm, endotherm, and plant species. The pattern also appears to hold true when intraspecific tolerances to cold versus heat are measured among a small number of *Liolaemus* lizard species in South America. These results extend to a wide variety of organisms the finding for some terrestrial ectotherms that, generally, lower thermal limits are far more labile than upper limits (e.g., Addo-Bediako et al. 2000; Boher et al. 2010; Sunday et al. 2011; Grigg and Buckley 2013; Hoffmann et al. 2013). For a smaller set of ectotherm and endotherm species we also show that critical limits to cold tend to correlate with metrics of ambient temperature, thus supporting the hypothesis that natural selection modulates physiological adaptation of species to lower temperatures. In contrast, critical limits to heat are, by and large, uncorrelated with metrics of environmental temperature partially supporting the hypothesis of conservatism of physiological tolerances to heat. These results extend to previous analysis the evidence provided for terrestrial ectotherms that lower thermal limits are generally correlated with latitude (an indirect variable expected to correlate with metrics of ambient temperature), whereas upper thermal limits show much less geographic variation (e.g., Addo-Bediako et al. 2000; Sunday et al. 2011; Grigg and Buckley 2013). In consequence, they also implicitly suggest that the differences in range dynamics among marine and terrestrial species in response to changing climates that have been identified previously on the basis of different asymmetries in tolerance (Sunday et al. 2012) may extend more broadly.

It might be argued, however, that phenotypic plasticity could reduce the extent of the differences in lability of upper and lower thermal tolerances. However, for a wide range of ectotherms evidence is accumulating that plasticity of upper limits is much reduced by comparison with plasticity of lower limits (Chown et al. 2006; Hoffmann et al. 2013). How common this is for endotherms and plants is not yet clear, although it deserves explicit investigation for reasons that will become clear below (see also Piersma and Drent 2003).

Asymmetry in conservatism between lower and upper thermal limits is likely to be the consequence of different physiological processes operating near critical lower and upper thermal limits. With animals, variation in lower thermal limits is a consequence of differences in thermodynamic effects of temperature on reaction rates, and most likely those responsible for maintaining ion homeostasis (e.g., Hosler et al. 2000; MacMillan et al. 2012). In contrast, variation in tolerance to heat is mostly a consequence of limited variation in the ability of organisms to counter the destabilizing effects of high temperature on membranes and proteins (for review see Angilletta 2009). The latter processes involves, *inter alia*, ancient polypeptides that are expected to be highly conserved across all forms of living organisms (e.g., Gupta and Golding 1993).

Likewise, cold acclimation of plants relies on adjusting metabolic processes (essentially photosynthesis and respiration) and on avoiding lethal freezing (e.g., Larcher 1995). Both aspects have been shown to be highly dynamic since plants not only adapt quickly to thermal environments but also acclimate and de-acclimate seasonally to low temperatures (e.g., Pagtera and Arorab 2013). Plants have also been shown to acclimate quickly to high temperatures (e.g., Sung et al. 2003). However, changes in lipid composition of the membranes and increased production of heat shock proteins, two basic processes involved in heat tolerance of plants, are typically not sufficient to enable them to cope with temperatures above 45 ºC, except in exceptional circumstances, such as in the case of desiccated state of resurrection plants (e.g., Larcher 1995; Kappen and Valladares 2007). Thus, as is the case with animals, sound physiological reasons exist to explain why plants are more likely to exhibit higher variability and adaptive potential in their lower rather than their upper limits of thermal tolerance.

Higher order processes likely set thermal limits in marine organisms (Pörtner 2001), (Pörtner 2001), often resulting in close matches between range limits and thermal tolerances, with important consequences for range dynamics (Sunday et al. 2012). Although higher order processes have also been claimed to set thermal limits in terrestrial ectotherms (Pörtner 2001), several studies suggest that the latter is unlikely (e.g., Klok et al. 2004; McCue and Santos 2013). These profound differences between marine and terrestrial groups may partly account for the differences in the associations between ranges and tolerances found in marine and terrestrial organisms, with ‘mismatches’ being more common in terrestrial species (see the detailed treatment of tolerances, range filling and the impacts of climate change by Sunday et al. 2012).

Clearly some organisms are able to develop substantial resistance to high temperatures, but this is rare (reviewed by Hoffmann et al. 2013). For example, lichens, bryophytes and vascular plants can increase their heat tolerance at decreasing water content, with some species being able to recover from temperatures exceeding 80 ºC and even 120 ºC if these are experienced in desiccated state (e.g., Kappen and Valladares 2007). The same is true of some of several anhydrobiotic invertebrates (e.g., Watanabe et al. 2002). Perhaps most notable are extremophilic microbes whose proteins can be synthesized at temperatures exceeding 100 °C (e.g., Kashefi and Lovley 2003). Several desert ant species are also known to tolerate temperatures exceeding 50 °C during short-term periods of activity (e.g., Wehner et al. 1992). However, the average upper thermal limit for insects in our data is 41.6 °C and temperatures above 47.8 °C are thought to be tolerated only temporarily by animals (Pörtner 2002).

In this context, an important question is whether complex terrestrial organisms can evolve hyperthermostability (the ability to maintain structural stability and function at high temperatures, e.g., >50 °C) under specific circumstances. Forecasts are forgoing increases in global temperatures that will, in many circumstances, exceed organismal upper thermal limits substantially constraining fitness (ultimately survival) (e.g., Wahid et al. 2007; Kearney et al. 2009; Bozinovic et al. 2011). If organisms are unlikely to be able to alter upper thermal limits, by whatever mechanism, then extinction risk may be much higher than currently anticipated. However, behavioural regulation and microclimate availability may still provide important opportunities for improvement of performance and survival.

Ultimately, the question is whether conservatism of upper thermal tolerances among terrestrial organisms is due to hard physiological boundaries that prevent adaptation of organisms beyond given temperature limits, whether it is due to biogeographical legacies that set the context for evolution, or whether selection for tolerance of rare temperature events might be responsible for it. The biogeographical argument is as follows: Earth's climate has been predominantly warm throughout its history with pulses of cold climates coming and going (e.g., Ruddiman 2001). The planet was at its coldest known state between 850 and 550 million years ago (mya), and complex organisms evolved after this period (e.g., Romdal et al. 2013). Subsequently, two major glaciations occurred: the first between 325 and 240 mya; and the second 35 mya at the onset of the Oligocene. A shorter glaciation might have also taken place at about 430 mya (Ruddiman 2001). However, the critical issue for evolution is that the equatorial region has remained warm through glacial interglacial cycles (between 30 °C and 40 °C between the Paleocene and the Pliocene, Figure 6), while higher latitudes were exposed to marked climatic variation (from nearly 0 °C to -80 °C, Figure 6). Thus, it is not surprising that the vast majority of clades evolved in the thermally stable and warm equatorial region (e.g., Jablonski et al. 2006; Romdal et al. 2013), while some clades were able to colonize higher latitudes via physiological adaptations to lower temperatures (e.g., Wiens and Donoghue 2004).

If the world remained warm during most of its history, with most species evolving in environments exposed to relatively high temperatures, better performance at higher temperatures (a thermodynamic effect—see, e.g., Asbury and Angilletta 2010) would be expected, and maximum performance temperatures would also be closer to thermal maxima than thermal minima owing to irreversible enzyme inactivation at higher temperatures (i.e., thermal responses would be negatively skewed, as is the case—see Kingsolver 2009).

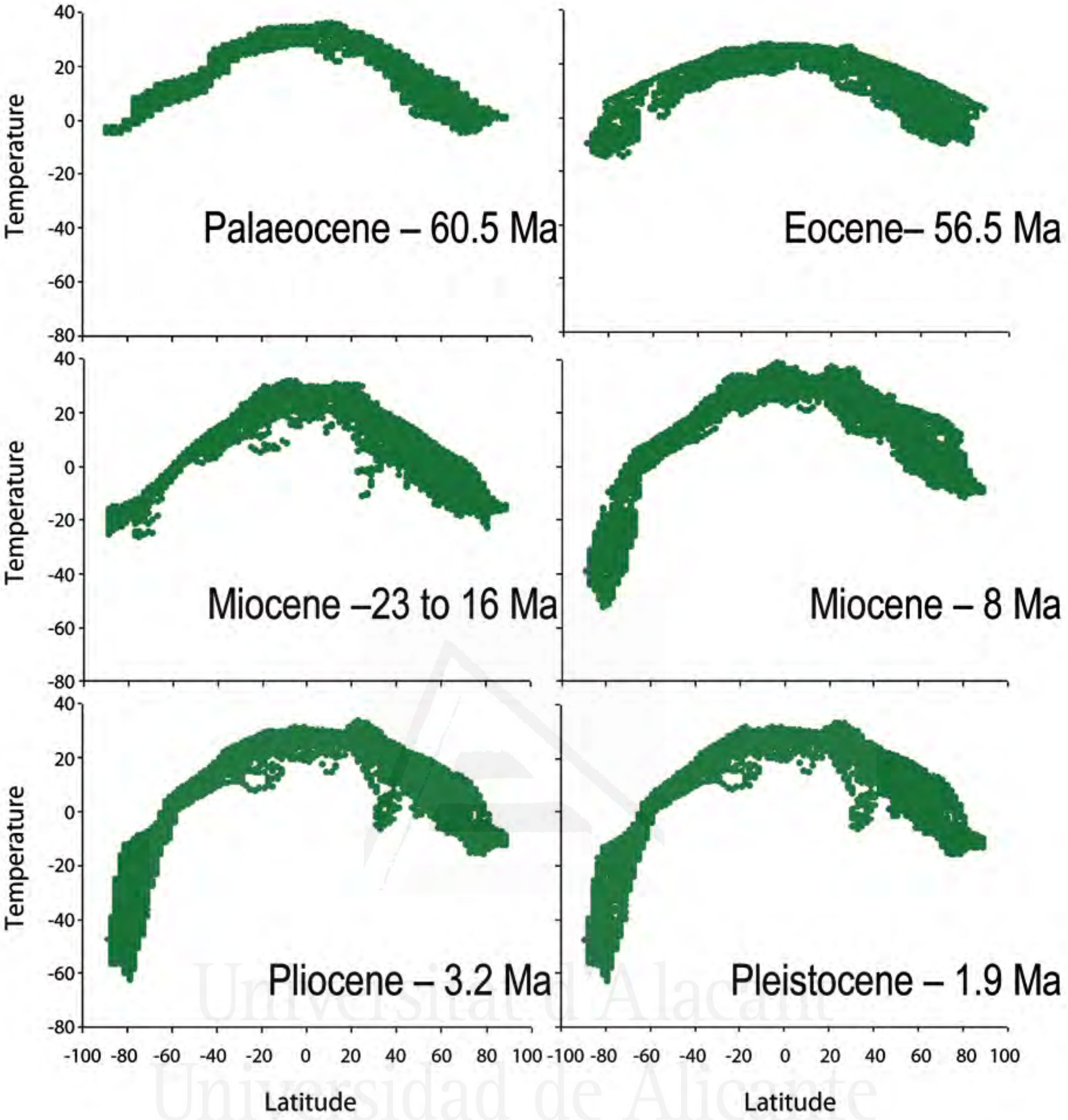

Figure 6. Changes in mean annual temperature values (°C) across latitude (°) from the Paleocene to the Pliocene. Raw data to build the figure was based on GCM simulation hindcasts kindly provided by Persaram Batra (Miocene 23-26) and Paul Valdes and Alan Haywood (Palaeocene, Eocene, Miocene 8, Pliocene 3.2 and 1.9).

Opportunities for speciation and evolution of thermal niches would thus occur through adaptive radiation in relatively colder and species poor areas (e.g., Gavrilets and Vose 2005). This reasoning could explain why most selective pressures favoured niche evolution in cold environments while little pressure existed for evolution of thermal niches in warm and stable environments (Donoghue and Moore 2003). However, it does not explain why so little evidence exists for thermal evolution above 50 ºC. For example why so few species survive in deserts and why those that survive typically do so by developing behavioural adaptations (a good example are the desert ants described by Wehner et al. 1992 that developed behavioural adaptations to heat rather than physiological adaptations).

Hard physiological boundaries, or selection for survival of rare, high extreme temperature at any latitude (absolute maximum temperatures vary much less across space than do absolute minima – see Addo-Bediako et al. 2000) are, at this stage, the two most plausible alternative explanations for them. Distinguishing among these alternatives has not been the subject of detailed research. However, the former is, in our view, most plausible given that so few metazoan organisms, even in extreme environments such as at marine hydrothermal vents (see, e.g., Ravaux et al. 2013), are able to exploit exceptionally hot, though energy rich, environments (i.e., much above 55 ºC). Nonetheless, it is clear that explicit consideration of these alternatives is an important area for research.

Indeed, given that a few metazoans and plants seem to have evolved mechanisms to overcome temperature extremes (see above, and also Girguis and Lee 2006), understanding the biochemical and genetic basis of this ability, and how it might be promoted in other groups, is clearly important for the further development of conservation strategies for adapting to on-going global temperature increases. Research in a variety of taxa is starting to address this question, especially from a genetic perspective, but consensus has yet to emerge (see Williams et al. 2012 for a brief overview). If upper thermal tolerance boundaries are indeed hard (or show limited ability to evolve), and the prospects for dispersal keeping pace with rates of change limited, then assisted migration (or managed relocation) may indeed become a preferred strategy, irrespective of its potential risks (e.g., Schwartz et al. 2012). By contrast, if upper boundaries are more malleable and can be altered through hybridization of populations or other approaches that might be considered a form of 'assisted evolution', then alternatives to wholesale relocations are plausible. Assisted evolution of domestic species has been a key component of human success, but has rarely been applied in this form in a conservation context (but see, e.g., Jones and Monaco 2009).

NICHE CONSERVATISM LEADS TO NICHE SIMILARITY

One of the conclusions that we reach from the observation of high conservatism of upper thermal limits among terrestrial organisms is that many species are unlikely to evolve physiological tolerances to increased heat, especially when their climatic preferences are close to their upper thermal limits. In such cases, evolution of physiological tolerances is impaired, and species persistence is challenged unless species have other means to adapt to increased environmental temperatures — a topic now being thoroughly investigated (Deutsch et al. 2008; Huey et al. 2009; Clusella-Trullas et al. 2011; Kellermann et al. 2012b; Sunday et al. 2012; Grigg and Buckley 2013; Hoffmann et al. 2013). But another, more general and largely unnoticed consequence of niche conservatism is that fundamental niches, or at least the thermal components of the fundamental niches, are likely to be more similar among closely related species than is usually inferred with methodologies that relate geographical distributions of species with aspects of climate.

The idea that tolerances of species to environmental gradients varies continuously along environmental gradients was first proposed by Robert H. Whittaker (Whittaker 1967).

His ideas led to the development of the theory of gradient analysis and the continuum concept in community ecology, whereby species should gradually substitute each other along environmental gradients due to varying individual preferences and tolerances (see also Austin 1985). Even though these ideas were developed based on extensive empirical analyses of plant species distributions, we show here that the type of response curves of species in relation to the environment that were obtained for plants (e.g., Whittaker 1967) are unlikely to be fundamentally different from the response curves obtained for animals (see Figure 7A). Indeed, the generality of such relationships has meant that the continuum concept underlies much of the thinking that motivates bioclimatic envelope modelling

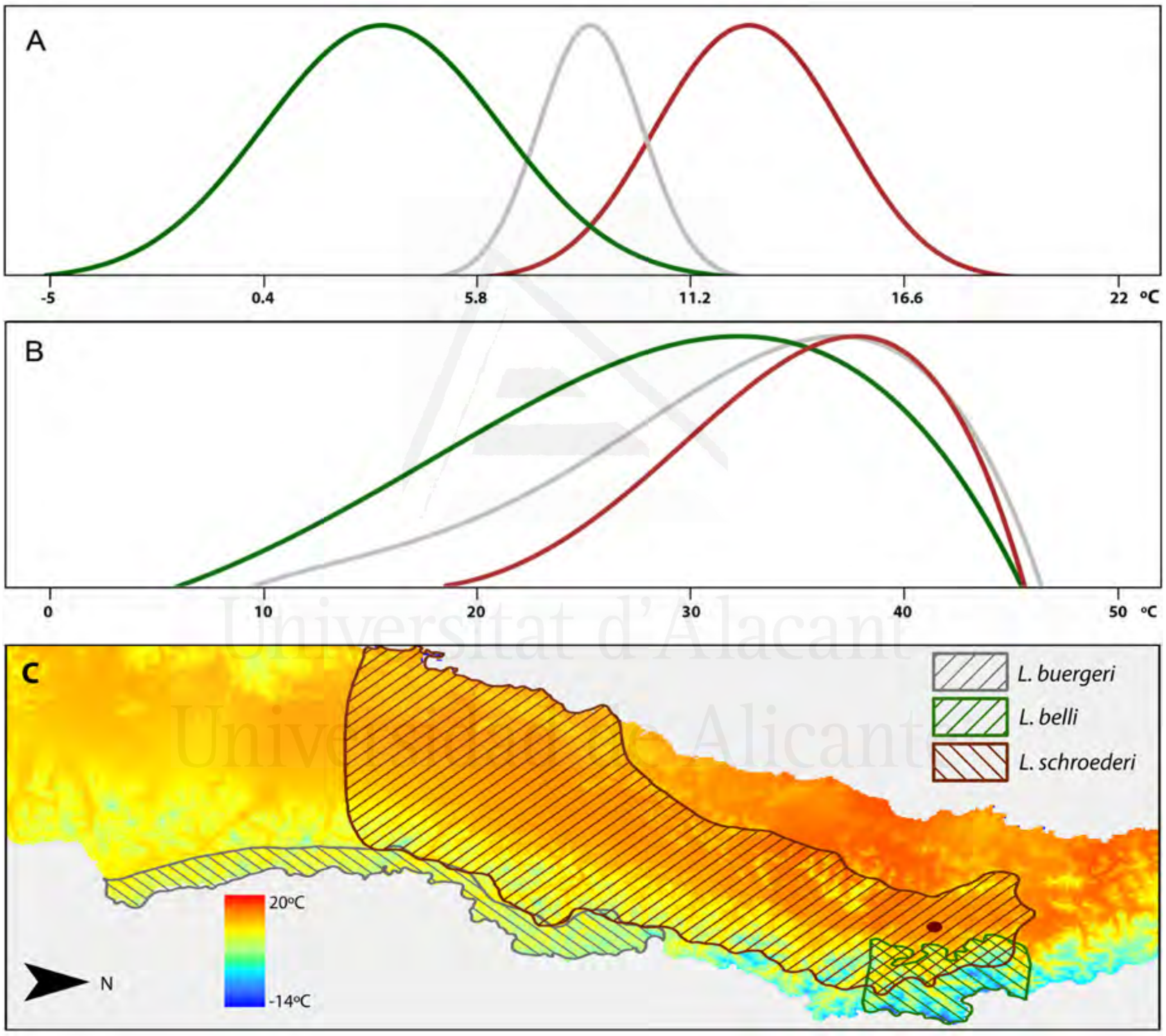

Figure 7. (A) Response curves estimated with bioclimatic envelope models (logistic regression) relating species distributions of three species of *Liolaemus* lizards in central Chile (see panel C) against mean annual air environmental temperatures (from Hijmans et al. 2005) (i.e., characterization of the realized niche for mean annual temperature); (B) empirical performance curves for the same species of *Liolaemus* (from F. Ferri-Yáñez, unpublished data) measured with sprint speed in laboratory conditions against body temperature (i.e., characterization of the fundamental niche for body temperature); and (C) geographical distributions of the three species of *Liolaemus* (from P.A. Marquet and C. Garín, unpublished data) overlaid on mean annual temperature.

(alternatively termed ecological niche modeling, habitat suitability modeling, or species distribution modeling; see for recent review of terminology Araújo and Peterson 2012), and that is used to infer species climatic niches based on associations between aspects of climate and species' geographical distributions (e.g., Austin 1985; Peterson et al. 2011). As shown in Figure 7B, however, niche conservatism can cause the metabolic (thermal) response curves of different species to be more similar than expected if climatic niches were inferred from analysis of geographical distributions and species occupancies of thermal gradients. Although varying levels of conservatism might exist among traits affecting different dimensions of the fundamental niches (e.g. tolerance to water), our extensive analysis of lower and upper thermal limits among terrestrial organisms is consistent with the proposition that fundamental niches, or at least their thermal component, should be more similar among species than typically inferred with methods that relate the geographical distributions of species with their environment.

Even though interspecific and intraspecific differences between fundamental niches are expected due to niche evolution and/or phenotypic plasticity (see also, e.g., Hoffmann et al. 2003; Klok and Chown 2003), we expected the thermal component of the fundamental niches to differ less within and among species than the thermal component of realized niches. Moreover, major interspecific and intraspecific differences between fundamental niches should be expected mainly at the tails of the species-temperature response curves, especially when these tails approach lower temperature limits (Figure 7B). In contrast, limited overlap between realized niches of closely related species is likely to be more common and a consequence of historical climatic legacies (e.g., Ricklefs 2006), the effects of biotic interactions (e.g., Dobzhansky 1950), limited dispersal (e.g., Baselga et al. 2012) and, perhaps, variation in species tolerances to aspects of the environment that are not characterized by, but may also influence responses to thermal gradients.

CONSEQUENCES OF NICHE SIMILARITY FOR STUDIES IN ECOLOGY AND EVOLUTION

The extent to which functional traits, performance currencies, and the environment, vary across clades is a central question in ecology and evolution (e.g., Messier et al. 2010). Our prediction that fundamental niches are more similar across lineages than inferred from analysis of realized niches is of critical importance for a range of research questions. For example, uncritical analysis of realized climatic niches can lead to important mistakes when predicting the effects of climate change on species distributions, assessing the risk of species invasion, or making inferences about rates of niche evolution. Specifically, if realized niches are highly constrained by dispersal, biotic interactions, and/or resource utilization, as they are expected to be at low latitudinal and altitudinal ranges (e.g., Dobzhansky 1950; Loehle 1998), then they are unlikely to provide accurate estimates of species tolerance limits to climate. When this is the case, projections from bioclimatic envelope models will have a tendency to overestimate the effects of climate change on species distributions, underestimate the risk of species invasions, and miscalculate rates of niche evolution. In contrast, if realized niches are mainly constrained by climate variables, as it expected to be the case at higher latitudes and altitudes, then greater similarity between realized niches and fundamental niches is expected with the consequence that bioclimatic envelope models are also more likely to provide accurate predictions. This outcome is most likely when thermal aspects of the environment-organism interaction are most significant, which is in any case often the outcome of many bioclimatic envelope models given the significance of the thermal environment for organisms (e.g., Walther et al. 2005; Kearney et al. 2010). Rates of environmental change may also play a role given differential organismal responses to them, particularly phenotypic plasticity (e.g., Terblanche et al. 2011), although plasticity is much less significant for upper thermal tolerance traits (see above).

Among the work done recently, a comprehensive example of the significance of understanding fundamental thermal limits in the context of species distributions is provided by Sunday et al. (2012). They show how differences in the way upper and lower limits vary among marine and terrestrial organisms have fundamental implications for understanding species distributions as climate continue to change. The *Liolaemus* lizards discussed above (see Figure 7) provide a further example. Assume, for the sake of argument that a reasonable and similar correlation exists between increases in ambient temperature and increases in the body temperature of the species. If ambient temperatures increased uniformly across the gradient, populations of *Liolaemus schroederi* at the upper tail of the temperature gradient would be the first to go extinct unless behavioural adaptations enabled them to persist under further warming (e.g., Huey et al. 2003). Assuming a similar interspecific relation between ambient and body temperatures, bioclimatic envelope models would be expected to correctly predict extinctions because the upper tail of the species-temperature response curve inferred with bioclimatic envelope models (Figure 7A) as the lizard temperature reaches the upper thermal tolerance of the species as measured under laboratory conditions (Figure 7B). In contrast, mismatches between the upper thermal tolerances and the upper tails of the species-temperature response curves, as is clear for the other two species, would cause failure of models to predict correctly extinctions under warming. For example, increased temperatures along the thermal gradient in Figure 7B would cause bioclimatic envelope models to shift to the right and predict losses of climate suitability within existing ranges of *Liolaemus belli* and *Liolaemus buergeri*. However, if species are exposed to temperatures below their preferred body temperatures, increases in ambient temperature will increase their fitness. That is, models inferring niches from assessments of the relationship between geography and the environment would have a tendency to overestimate extinction risk in a climate warming scenario.

When realized niches for closely related species are segregated along the temperature gradient (Figure 7A) and thermal fundamental niches are overlapping for them (Figure 7B), one implication is that several regions with suitable climate for the species are likely to be unoccupied. A low degree of equilibrium of species distributions with climate has already been reported for ectotherms (e.g., Munguía et al. 2012), endotherms (e.g., Monahan and Tingley 2012), and plants (e.g., García-Valdés et al. 2013), and one of the consequences for modelling of invasive species outside of their native ranges is that models will underestimate the extent of the areas that can be invaded. Another consequence is that tests of predictive success of models across invaded ranges will tend to generate high omission errors (invaded areas not predicted to be invaded by models) (e.g., Broennimann et al. 2007; Fitzpatrick et al. 2007) and these may invite potentially erroneous interpretations of shifts in the fundamental niches. A pragmatic solution to improve inferences of physiological limits based on geographical distributions of species, is to model species distributions using both native and invaded ranges (Broennimann and Guisan 2008) or, whenever possible, use historical distributional records (e.g., Nogués-Bravo et al. 2008).

Studies in evolution are also bound to be strongly affected by overestimation of niche differences across lineages. Specifically, if the currency of interest is rates of change in physiological aspects of the niche (e.g., Peterson et al. 1999; Hof et al. 2010; Kozak and Wiens 2010), then overestimation of niche differences among species will lead to inflation of evolutionary rates of the niche and this will lead to erroneous conclusions about niche conservatism and its importance in driving biodiversity patterns on earth.

CONCLUDING REMARKS

The activity of terrestrial animals and plants is limited by their thermal environment. Because environmental temperature varies in time and space, sometimes abruptly, organisms are continually challenged to maintain homeostasis. Here, we asked if physiological adaptation of species to current climate warming was likely, and what the consequences might be if this was not the case. For a large number of terrestrial ectotherms, endotherms and plants, we show that interspecific variation for lower thermal limits is greater than for upper limits. Similar patterns were found among individuals of the same species for a small number of South American lizard species, suggesting that selection could act at intraspecific level for lower thermal tolerances in cold environments while reduced opportunities might exist for selection of upper tolerances under warm conditions. We also found for a sample of ectotherm and endotherm species that lower limits of tolerance tend to covary with ambient temperature, whereas upper thermal limits tend not to. In other words, natural selection seems to modulate physiological responses to lower temperatures more so than it does at upper temperatures. Two conclusions can be drawn from these results. First, rates of niche evolution vary for different traits. The implication is that controversy regarding rates of niche evolution versus conservatism cannot be settled unless specific predictions are made and tested for different traits. Although similar statements have been made previously (e.g., Slobodkin and Rapoport 1974), the consequences of this reasoning for the niche conservatism debate have not always been fully appreciated (see for discussion Araújo and Peterson 2012). Second, and more importantly, hard boundaries seem to constrain evolution of upper thermal tolerances beyond given temperature limits. One consequence of strong conservatism of upper thermal limits among terrestrial organisms is that fundamental niches, particularly the upper tails of species-temperature response curves, should be more similar among closely related species than typically inferred with bioclimatic envelope models or with multivariate approaches relating species distributions with environmental predictors (e.g., Hof et al. 2010; Kozak and Wiens 2010). Thus, realized niches of species living in cold environments will tend to underestimate upper thermal limits, potentially causing models to overestimate the effects of climate warming on biodiversity (see also Sunday et al. 2012). In contrast, realized niches for species in warm environments are closer to their physiological upper thermal limits. In such cases, further climate warming will cause models to predict correctly range contractions, unless species have other means to adapt to increased temperatures.

Improving understanding of the linkages between organisms and environments is critical for understanding rates of the evolution of niches, predicting the effects of climate change on biodiversity, and estimating the risk of invasive species (e.g., Wiens et al. 2010). To make progress in this field, greater interaction between otherwise disconnected disciplines is required. Specifically, there is need for greater coordination between empirical and theoretical research programs that characterize the fundamental niches of species, and these efforts need to feed into the development of models of species geographical distributions that more explicitly account for the physiological mechanisms constraining species distributions (e.g., Buckley et al. 2010; Sunday et al. 2012). Only with improved characterization of the physiological constraints on species distributions will researchers be able to quantify the additional contributions of non-climatic factors, such as dispersal and biotic interactions, in shaping ecological niches and geographic distributions.

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SUPPORTING INFORMATION

Figure S1
Figure S2
Table S1
Table S2
Table S3
Table S4
Table S5
Table S6
Thermal tolerance of *Liolaemus*
Details on Figure 7
Dataset 1

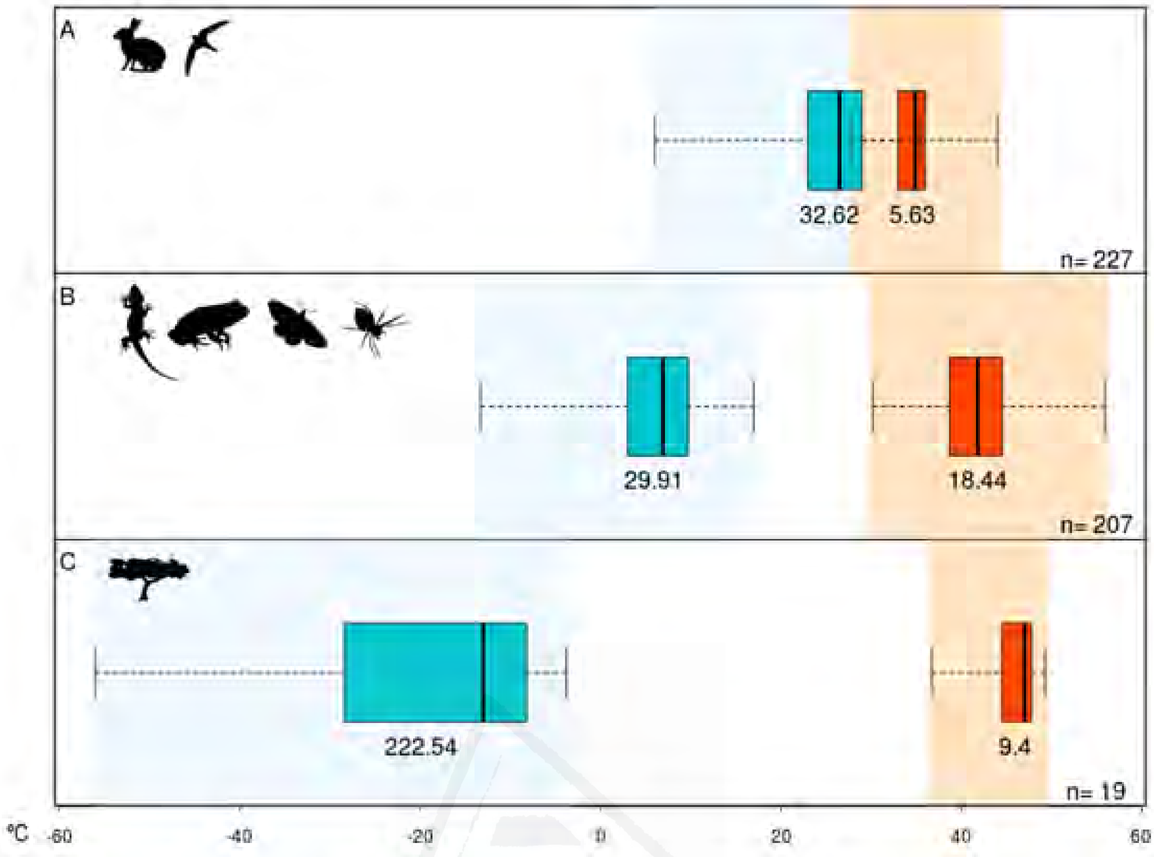

Figure S1. Ectotherms, endotherms, plants: A general graph using all paired data for endotherms (A), ectotherms (B) and plants (C). Variances are depicted below every boxplot, number of species (n) is on the lower right section of the graph.

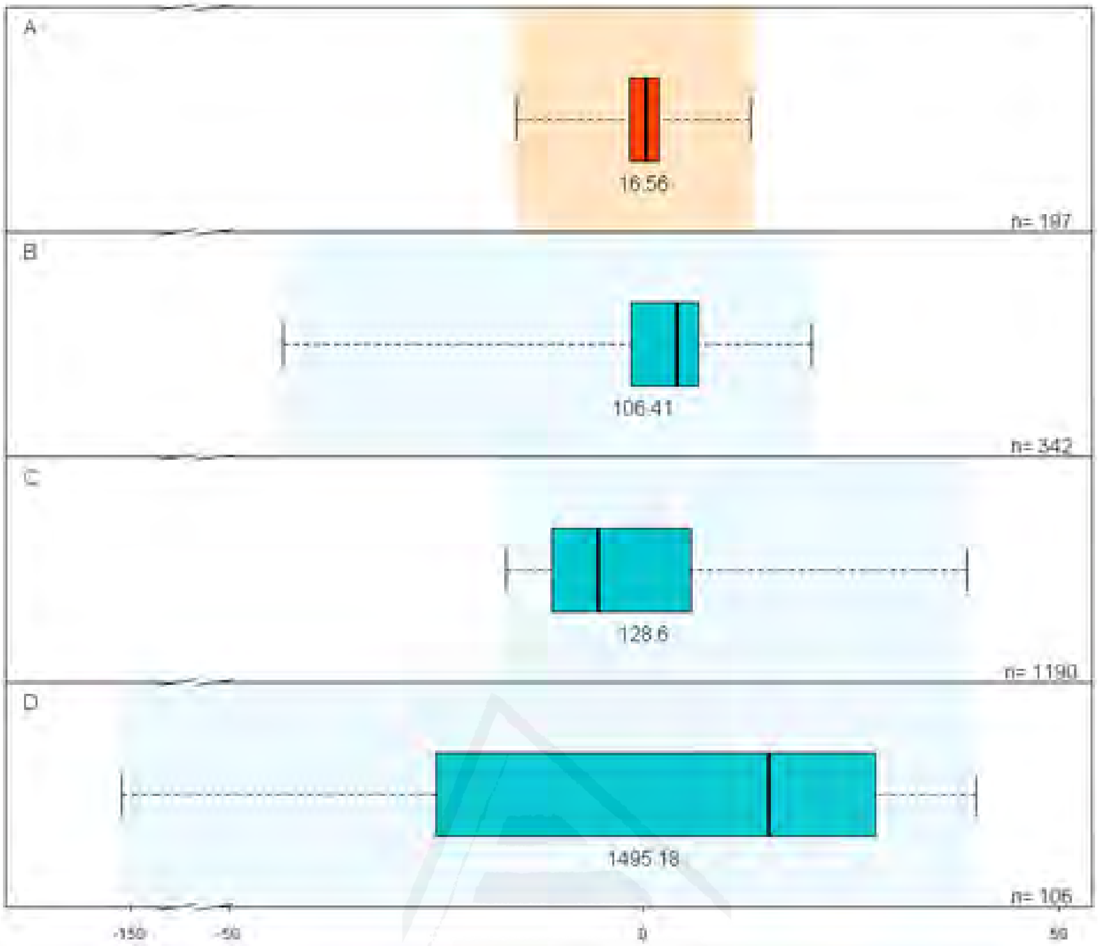

Figure S2. Plant heat tolerance (A) and cold tolerance (B) for all species (as in Figure 4), plus cold hardiness from hardiness zones (C) and maximum frost resistance (D). The data are normalized to the mean (so 0 represents the mean of each dataset) but not to the variances. Both paired and unpaired data were used. As in Figure S1 Variances are depicted below every boxplot, number of species (*n*) is on the lower right for the paired data and below each variance for the unpaired data.

Table S1. Summary statistics and source of the data used in fig.1 CT: Critical Temperature, LT50: Lethal Temperature for 50% of the population. LT100: Lethal temperature for 100% of the population. CT_{max}: Critical Thermal Maximum, CT_{min}: Critical Thermal Minimum, SD: (Sunday et al. 2012). HF: (Hoffman et al. 2013), DEU:(Deutsch et al. 2008). FFY: Francisco Ferri-Yáñez, Unpublished, KL: (Kellermann et al. 2012).

PAIRED DATA USED IN FIGURE 1A

		CT_{max}			CT_{min}			Source
CLASS	N	Mean	Var	Sd	Mean	Var	Sd	
Amphibia	26	37.52	11.26	3.35	2.80	20.70	4.55	SD
Reptilia	129	42.16	8.23	2.87	7.77	13.03	3.61	SD
Arachnida	12	40.85	2.64	1.63	-9.84	16.71	4.09	SD
Insecta	56-40	40.79	29.00	5.39	2.80	41.09	6.41	SD/HF

PAIRED DATA USED IN FIGURE 1B

Insecta	38	32.66	13.82	3.72	10.01	30.63	5.53	DEU

UNPAIRED INSECT DATA USED IN FIGURE 1C

		Maximum				Minimum			Source
MEASURE	N	Mean	Var	Sd	N	Mean	Var	Sd	
CT	220	41.83	21.53	4.37	31	2.49	13.31	3.65	HF/KL
LT50	89	36.73	42.40	6.51	215	-7.85	76.95	8.78	HF
LT100	84	40.08	58.80	7.67	108	-14.99	234.41	15.31	HF

PAIRED DATA USED IN FIGURE 1D

Reptilia	254	44.99	1.67	1.29	7.37	8.26	2.87	FFY

Table S2. Summary statistics for paired data from Sunday et al. 2012 and Hoffman et al. 2013 on thermal limits of ectotherm orders.

			CT_{max}			CT_{min}	
ORDER	N	Var	Mean	Sd	Var	Mean	Sd
Acarina	2	0.08	39.70	0.28	1.62	-6.00	1.27
Anura	26	11.26	37.52	3.36	20.70	2.80	4.55
Araneae	10	2.87	41.09	1.69	16.30	-10.61	4.04
Coleoptera	31	48.61	41.38	6.97	55.21	1.82	7.43
Collembola	3	3.09	33.80	1.76	10.09	-9.63	3.18
Diptera	14	8.59	38.13	2.93	27.06	4.64	5.20
Hemiptera	3	0.56	39.50	0.75	2.41	2.27	1.55
Hymenoptera	10	17.86	41.67	4.23	25.30	5.17	5.03
Isoptera	3	2.57	46.25	1.60	8.69	4.93	2.95
Lepidoptera	7	59.45	45.75	7.71	49.22	4.80	7.02
Squamata	134	8.26	42.13	2.87	13.49	7.70	3.67

Table S3. Summary statistics for plant tolerances.

		CT_{max}				CT_{min}		
DATASET	N	Var	Mean	Sd		Var	Mean	Sd
LT50 paired	19	9.4	45.89	3.07	19	222.54	-19.88	14.92
LT50 unpaired	178	17.18	47.33	4.15	323	96.86	-12.09	9.84
Hardiness	--	--	--	--	1190	128.6	-28.93	11.34
Frost Resistance	--	--	--	--	106	1495.18	-44.98	38.67

Table S4. Summary statistics for Lower Critical Temperature (LCT) and Upper Critical Temperature (UCT) of endotherms.

		LCT			UCT		
CLASS	N	Var	Mean	Sd	Var	Mean	Sd
Mammalia	157	3.53	34.21	1.88	26.24	26.21	5.12
Aves	70	9.50	35.38	3.08	42.80	23.61	6.54
Mammalia+Aves	227	5.63	34.57	2.37	32.62	25.4	5.71

Table S5. Spearman correlations and significance between thermal limits and environmental temperature as in Figure 5.

TOLERANCE MEASURE	CLIMATIC VARIABLE	REPTILES		AMPHIBIANS		INSECTS	
		ρ	*P*-value	ρ	*P*-value	ρ	*P*-value
CT_{max}	MaxTa	-0.495	3.716e-05	0.498	0.010	0.336	0.039
	MeanTa	0.035	0.785	0.109	0.595	0.241	0.144
	MinTa	-0.294	0.019	-0.099	0.630	0.145	0.384
CT_{min}	MaxTa	0.291	0.020	0.436	0.026	0.237	0.151
	MeanTa	0.303	0.016	0.745	1.29e-05	0.285	0.082
	MinTa	0.307	0.014	0.676	0.0002	0.188	0.257

Table S6. Spearman correlations and significance between thermal limits and environmental temperature for endotherms as in Figure 5.

TOLERANCE MEASURE	CLIMATIC VARIABLE	MAMMALS		BIRDS	
		ρ	*P*-value	ρ	*P*-value
UCT	MaxTa	0.196	0.083	0.286	0.197
	MeanTa	0.304	0.006	0.040	0.859
	MinTa	0.302	0.007	0.031	0.892
LCT	MaxTa	0.075	0.511	0.408	0.059
	MeanTa	-0.012	0.915	0.350	0.111
	MinTa	-0.058	0.614	0.315	0.153
Resid L	MaxTa	0.175	0.122	0.422	0.050
	MeanTa	0.071	0.531	0.333	0.130
	MinTa	0.028	0.809	0.071	0.531

Thermal tolerance of *Liolaemus*

CT_{min} and CT_{max} of Chilean *Liolaemus* were determined by loss of righting response. Most of the species were captured in a single location by F. Ferri-Yáñez or in several nearby locations and in the same period of time (per species), which gives confidence that individuals of each species experienced similar climatic conditions prior to the capture. All specimens were maintained in identical conditions in the laboratory with availability of water, food (mealworms), a thermoregulatory spot and a photoperiod of 12 hours of light for two days before measurements were taken.

Details on Figure 7

Logistic Regression

We used range maps built by C. Garín and P.A. Marquet representing the distribution of *Liolaemus buergeri*, *Liolaemus schroederi* and *Liolaemus belli* in shapefile format. Annual mean temperature maps were downloaded from www.worldclim.org (bioclimatic variable bio1). Distribution data was integrated in a 10 km grid in which each cell was marked as presence if it was covered in more than 50% by the range map; Annual Mean Temperature was integrated in the database using the average pixel value in every grid cell. Logistic regression model was conducted in R version 2.12.2 using annual mean temperature as independent variable.

Performance Curves

Performance curves were estimated by fitting a polynomial function to lizard sprint speed measures at eight different temperatures. Ten individuals of each species were chased through a 2 m long racetrack divided in 30 cm intervals and recorded at 60 frames per second with a high definition digital camera (GoPro® HERO2) at zenith angle. Recordings were reviewed visually frame by frame and the fastest interval was extracted for each race. Further details on the methods are to be published in Ferri-Yáñez et. al. in preparation.

Endotherm data (TNZ)

The Thermoneutral zone (TNZ) is the range of ambient temperatures for which metabolism of endotherms remains constant and lowest, as thermal balance can be maintained by changes in posture, insulation and peripheral circulation (McNab 2012). Outside the limits of TNZ, endotherms are forced to use energy requiring mechanisms to regulate their body temperature, either by increasing heat production if temperature is below TNZ or by active cooling mechanisms such as sweating or panting when temperature is above TNZ, causing an increase in metabolic rate. We reviewed the literature for TNZ boundaries and constructed a database of paired Lower Critical Temperatures (LCT) and Upper Critical Temperatures (UCT) for birds and mammals (Table S1).

We report and analyze the differences in variance between LCT and UCT, as we consider that it best represent the interaction between the species and the thermal environment. Nevertheless, basal metabolic rate and LCT have an allometric relation with body mass. We examined the relation between LCT and UCT with body mass, and as expected we found a negative correlation between LCT and body mass for both birds and mammals. To account for the effect of mass, we fitted a linear model to LCT and body mass for birds and for mammals separately and examined if the pattern of variance of the residuals. Variance of the residuals for both birds and mammals is still much larger than variance in UCT (bird residuals variance: 30.53, mammal residuals variance: 21.1)

Plant data

Plant physiological tolerances (LT50) were gathered from the literature (references provided). Besides the physiological data, we also obtained cold hardiness from compilations combining geographic information and hardiness zones from available databases at Compleat Botanica (www.crescentbloom.com), Planfor (www.planfor.co.uk), Plants of the Southwest (www.plantsofthesouthwest.com), Garden Web (www.uk.gardenweb.com/), and forestry and botanical information from national or regional repositories at the United States Department of Agriculture Natural Resources Conservation Service (http://plants.usda.gov), the North Carolina State University Cooperative Extension (www.ces.ncsu.edu), the European Forest Genetic Resources Programme (www.euforgen.org/distribution_maps.html), and the Australian National Botanic Gardens web portal (http://www.anbg.gov.au). Absolute maximum frost tolerance of plant tissues was obtained from Bannister & Neuner 2001. Variance of the different cold tolerance measures was close to one order of magnitude bigger in cold tolerance and cold hardiness, and close to two orders of magnitude bigger in maximum frost resistance than that of heat tolerance (Figure S1)

Dataset 1. Thermo Neutral Zone (Lct-Uct range) of mammals and bird species. Ref: bibliographic reference number.

Sp	*Tlc*	*Tuc*	Class	Order	Family	Weight g.	Ref
Abrothrix andinus	27	34	Mammalia	Rodentia	Cricetidae	34.6	6
Abrothrix longipilis	27	32	Mammalia	Rodentia	Cricetidae	42.3	6
Aethomys namaquensis	26.39	34.49	Mammalia	Rodentia	Muridae	64.2	32
Akodon azarae	30	32	Mammalia	Rodentia	Cricetidae	25	10
Arctictis binturong	27	36	Mammalia	Carnivora	Viverridae	1428	39
Auliscomys boliviensis	24	31	Mammalia	Rodentia	Cricetidae	76.8	6
Auliscomys micropus	22	33	Mammalia	Rodentia	Cricetidae	62.3	6
Caluromys derbians	26.36	35	Mammalia	Didelphimorpha	Didelphidae	357	2
Canis dingo	10	32.5	Mammalia	Carnivora	Canidae	18066.7	49
Cannomys badius	26.74	34.5	Mammalia	Rodentia	Spalacidae	344	3
Capromys pilorides	24	37	Mammalia	Rodentia	Hystricomorpha	2630	4
Cebuella pygmaea	27	34	Mammalia	Primates	Callitrichidae	153	56
Cercartetus lepidus	29	33	Mammalia	Diprotodontia	Burramyidae	12	21
Clethrionomys californicus	25	33	Mammalia	Rodentia	Cricetidae	18.3	38
Clethrionomys gapperi	26	34	Mammalia	Rodentia	Cricetidae	20.8	38
Coendou prehensilis	21.86	34	Mammalia	Rodentia	Erethizontidae	3280	4
Crocidura russula	27.5	35	Mammalia	Eulipotyphla	Soricidae	10.4	51
Crocidura suaveolens	27.5	35	Mammalia	Eulipotyphla	Soricidae	6.5	51
Ctenomis talarum	25	30	Mammalia	Rodentia	Ctenomyidae	116	12
Dasyprocta azarae	18	35	Mammalia	Rodentia	Dasyproctidae	3849	1
Didelphis virginiana	21.16	34	Mammalia	Didelphimorpha	Didelphidae	3257	2
Dipodomys deserti	29.5	35	Mammalia	Rodentia	Heteromydae	106	2
Dipodomys microps	27	32	Mammalia	Rodentia	Heteromydae	55	9
Dobsonia minor	27.5	35	Mammalia	Chiroptera	Pteropodidae	73.7	41
Dobsonia praedatix	26.5	33.5	Mammalia	Chiroptera	Pteropodidae	179.5	41
Dolichotis salinicola	28	37	Mammalia	Rodentia	Cavidae	1613	1
Elephantulus edwardi	32.5	36	Mammalia	Macroscelidea	Macroscelididae	48.1	31
Eutamias minimus	26	34	Mammalia	Rodentia	Sciuridae	50.6	55
Vulpes zerda	23.4	32	Mammalia	Carnivora	Canidae	1.1	53
Geomys pinetis	26	35	Mammalia	Rodentia	Geomyidae	202.8	37
Gerbillurus paeba	33.25	35.64	Mammalia	Rodentia	Muridae	31.13	11
Gerbillurus paeba paeba	32.3	35.1	Mammalia	Rodentia	Muridae	33.9	19
Gerbillurus seizeri	32.2	34.8	Mammalia	Rodentia	Muridae	46.1	19
Gerbillurus tytonis	32.4	34.9	Mammalia	Rodentia	Muridae	29.9	19
Gerbillurus vallinus vallinus	33.1	35	Mammalia	Rodentia	Muridae	38.8	19
Gerbillus dasyurus	32	35	Mammalia	Rodentia	Muridae	27.6	24
Gerbillus pusillus	31.4	38	Mammalia	Rodentia	Muridae	12.6	10
Graomys griseoflavus	25.6	34	Mammalia	Rodentia	cricetidae	69.4	15
Heliophobius kapeti	28	33	Mammalia	Rodentia	Bathyerginae	88.5	37
Heterocephalus glaber	31	37	Mammalia	Rodentia	Bathyerginae	39.2	37
Hipposideros diadema	29	34	Mammalia	Chiroptera	Hipposideridae	37.2	58
Homo sapiens	28.5	32	Mammalia	Primates	Hominidae	73600	26
Hydrochaeris hydrochaeris	22	33	Mammalia	Rodentia	Cavidae	26400	1
Jaculus orientalis	28	33	Mammalia	Rodentia	Dipodidae	139	10
Lagurus curtatus	25	33	Mammalia	Rodentia	Cricetidae	30.3	38
Leggadina hermannsburgensis	31	36	Mammalia	Rodentia	Muridae	12.2	34
Lemur fulvus	30	40	Mammalia	Primates	Lemuridae	2330	56

Sp	*T*lc	*T*uc	Class	Order	Family	Weight g.	Ref
Leopardus pardalis	22	33	Mammalia	Carnivora	Felidae	10500	40
Leopardus wiedii	29	38	Mammalia	Carnivora	Felidae	3600	40
Leptonycteris sanborni	35.5	38	Mammalia	Chiroptera	Phyllostomidae	44	14
Liomys salvani	31	34	Mammalia	Rodentia	Heteromydae	44	10
Lutreolina crassicaudata	26.37	35	Mammalia	Didelphimorpha	Didelphidae	812	2
Macaca fuscata	32.5	35	Mammalia	Primates	Cercopithecidae	9.55	44
Macaca mulatta	10	31	Mammalia	Primates	Cercopithecidae	3.9	16
Macroderma gigas	30	35	Mammalia	Chiroptera	Megadermatidae	150	30
Macroscelides proboscideus	35	38	Mammalia	Macroscelidea	Macroscelididae	45	48
Macrotis lagotis	27	35	Mammalia	Peramelemorphia	Thylacomyidae	1520	27
Manis javanicus	23	34	Mammalia	Pholidota	Manidae	2110	42
Marmosa robinsoni	26.79	37	Mammalia	Didelphimorpha	Didelphidae	122	2
Melonycteris melanops	28	33	Mammalia	Chiroptera	Pteropodidae	53.3	59
Metachirus nudicaudatus	27.65	35.5	Mammalia	Didelphimorpha	Didelphidae	336	2
Microtus longicaudus	26.5	33.5	Mammalia	Rodentia	Cricetidae	26.9	38
Monodelphis brevicaudata	28.76	36	Mammalia	Didelphimorpha	Didelphidae	111	2
Mus musculus	27	33	Mammalia	Rodentia	Muridae	46	10
Myoprocta acouchy	25	30	Mammalia	Rodentia	Dasyproctidae	914	1
Myotis tisanoides	32.5	34.5	Mammalia	Chiroptera	Vespertilionidae	8.4	46
Nandinia binoata	27	34	Mammalia	Carnivora	Nandiniidae	4270	39
Napaeozapus insignis	30	34	Mammalia	Rodentia	Dipodidae	22	10
Nasua nasua	25	33	Mammalia	Carnivora	Procyonidae	3.85	17
Neofiber alleni	25	34	Mammalia	Rodentia	Cricetidae	258.1	38
Neotoma lepida	31	35	Mammalia	Rodentia	cricetidae	106	45
Notomys alexis	32	34	Mammalia	Rodentia	Muridae	32.3	33
Nycticebus pygmaeus	27.5	35	Mammalia	Primates	Lorisidae	388	56
Nycticebys coucang	25	33	Mammalia	Primates	Lorisidae	1300	56
Nyctimene albiventer	28	33.5	Mammalia	Chiroptera	Pteropodidae	30.9	41
Ochrotomys nuttali	30	36	Mammalia	Rodentia	Cricetidae	20	10
Octodon bridgesi	22	32.5	Mammalia	Rodentia	Octodontidae	176.1	7
Octodon degus	27	35	Mammalia	Rodentia	Octodontidae	206	1
Octodon lunatus	23	33	Mammalia	Rodentia	Octodontidae	173.2	7
Octodontomys gliroides	25	35	Mammalia	Rodentia	Octodontidae	152	1
Ondatra zibethicus	15	30	Mammalia	Rodentia	Cricetidae	1004.6	38
Onychomys torridus	30	35	Mammalia	Rodentia	Cricetidae	19.1	54
Orycteropus afer	26	34	Mammalia	Tubulidentata	Orycteropodidae	48000	42
Oxymycterus roberti	33	34	Mammalia	Rodentia	Cricetidae	83.5	42
Panthera leo	9	33	Mammalia	Carnivora	Felidae	98000	40
Panthera onca	10	36	Mammalia	Carnivora	Felidae	50400	40
Pardoxurus hermaphroditus	27	36	Mammalia	Carnivora	Viverridae	3160	39
Perodicticus potto	25	29	Mammalia	Primates	Lorisidae	1090	56
Perognathus intermedius	33	36	Mammalia	Rodentia	Heteromydae	14.9	8
Peromyscus californicus insignis	28	34.5	Mammalia	Rodentia	Cricetidae	45.5	36
Peromyscus californicus parasiticus	27	34.5	Mammalia	Rodentia	Cricetidae	49.6	36
Peromyscus critinus pergracilis	29	35	Mammalia	Rodentia	Cricetidae	20.9	36
Peromyscus critinus stephensi	28.5	35	Mammalia	Rodentia	Cricetidae	15.9	36
Peromyscus eremiscus eremiscus	30	36.5	Mammalia	Rodentia	Cricetidae	21.5	36
Peromyscus m. gambeli	29	34.5	Mammalia	Rodentia	Cricetidae	19.1	36
Peromyscus m. sonoriensis	29	32	Mammalia	Rodentia	Cricetidae	24.2	36
Peromyscus t. gilberti	27	33	Mammalia	Rodentia	Cricetidae	33.3	36
Peromyscus t. truei	29	34.5	Mammalia	Rodentia	Cricetidae	33.2	36

Sp	*Tlc*	*Tuc*	Class	Order	Family	Weight g.	Ref
Peromyscus thomasi	28	35	Mammalia	Rodentia	Cricetidae	111	10
peromyscus truei gilberti	27	33	Mammalia	Rodentia	Cricetidae	33	10
Peropteryx macrotis	30.5	37	Mammalia	Chiroptera	Emballonuridae	5	22
Philander opossum	28.98	36	Mammalia	Didelphimorpha	Didelphidae	751	2
Phyllotis darwini	27.5	34	Mammalia	Rodentia	Cricetidae	59	6
Potos flavus	25	33	Mammalia	Carnivora	Procyonidae	2030	39
Procavia capensis	20	30	Mammalia	Hyracoidea	procaviidae	3457	43
Pseudocheirus occidentalis	25	32.5	Mammalia	Diprotodontia	Pseudocheriridae	872	27
Pteronotus quadridens	30	38	Mammalia	Chiroptera	Mormoopidae	4.9	47
Pteropus rodricensis	24	35.5	Mammalia	Chiroptera	Pteropodidae	254.5	41
Pteropus scapulatus	24	35	Mammalia	Chiroptera	Pteropodidae	440	5
Puma concolor	9	35	Mammalia	Carnivora	Felidae	37200	40
Rattus norvegicus	25	31	Mammalia	Rodentia	Muridae	160	10
Rattus rattus	26.25	33	Mammalia	Rodentia	Muridae	225	20
Rattus villosissimus	29	34	Mammalia	Rodentia	Muridae	134	20
Reithrodontomys megalotis	33	35	Mammalia	Rodentia	Cricetidae	9	10
Scalopus aquaticus	25.15	33	Mammalia	Soricomorpha	Talpinae	48	3
Setonix branchyurus	20	32.5	Mammalia	Diprotodontia	Macropodidae	2674	27
Spalacopus cyanus	26.53	34.5	Mammalia	Rodentia	Hystricomorpha	185	3
Spilogale putorius	30	36	Mammalia	Carnivora	Mephitidae	624	28
Tachyglossus aculeatus lawesi	24	33	Mammalia	Monotremata	Tachyglossidae	2140	42
Tachyglossus aculeatus setosus	18	31	Mammalia	Monotremata	Tachyglossidae	3580	42
Tachyoryctes splendens	27	35	Mammalia	Rodentia	Spalacidae	202.5	37
Tamandua tetradactyla	23	35	Mammalia	Pilosa	Myrmecophagidae	3500	42
Tamias striatus	28.5	32	Mammalia	Rodentia	Sciuridae	92.2	18
Thallomys paedulcus	27.46	35.89	Mammalia	Rodentia	Muridae	132.42	32
Thomomys talpoides	26	32	Mammalia	Rodentia	Geomyidae	106.8	23
Tupaia belangeri	27.5	35	Mammalia	Scandentia	tupaiidae	120.67	56
Zaglossus bruijni	18	33	Mammalia	Monotremata	Tachyglossidae	10300	42
Aegotheles cristatus	31.3	34.8	Aves	Caprimulgiformes	Aegothelidae	45	67
Amphispiza belli nevadensis	28	37	Aves	Passeriformes	Emberizidae	18.6	76
Anas gracilis	30	39	Aves	Anseriformes	Anatidae	393.7	74
Aramides cajanea	31	38	Aves	Gruiformes	Rallidae	374.3	75
Aulacorhynchus sulcatus	23	31	Aves	Coraciformes	Bucerotidae	131.7	73
Baeolophus ridgwayi	17.1	35.7	Aves	Passeriformes	Paridae	16.6	65
Callipepla californica	27.5	37.5	Aves	Galliformes	Odontophoridae	149.6	63
Ceococcyx californianus	27	36	Aves	Cuculiformes	Cuculidae	284.7	69
Cinclus mexicanus	11.5	34	Aves	Passeriformes	Cinclinae	50.2	77
Collocalia esculenta	31.5	34	Aves	Apodiformes	Apodidae	6.8	84
Collocalia vanikorensis	30	34	Aves	Apodiformes	Apodidae	11.6	84
Columba livia	23	36	Aves	Columbiformes	Columbidae	314.6	69
Columba vitiensis	22	34	Aves	Columbiformes	Columbidae	467.9	71
Cyanoramphus auriceps	22	37	Aves	Psittaciformes	Psittacidae	52.9	83
Cyanoramphus novaezelandiae	22	37	Aves	Psittaciformes	Psittacidae	56.1	83
Cyanoramphus unicolor	18	33	Aves	Psittaciformes	Psittacidae	129.4	83
Ducula pacifica	27.5	35	Aves	Columbiformes	Columbidae	333.4	71
Ducula pistrinaria	27	35	Aves	Columbiformes	Columbidae	394.2	71
Ducula zoeae	19	32	Aves	Columbiformes	Columbidae	602.3	71
Fulica atra	20	34	Aves	Gruiformes	Rallidae	842.5	70
Gallinula mortierii	15	35	Aves	Gruiformes	Rallidae	954.4	75
Gallirallus owstoni	28	38	Aves	Gruiformes	Rallidae	198.8	75

Sp	*T*lc	*T*uc	Class	Order	Family	Weight g.	Ref
Gymnophaps albertisii	22	36	Aves	Columbiformes	Columbidae	241	71
Hemiphaga novaeseelandiae	20	30	Aves	Columbiformes	Columbidae	443	71
Lichmera indistincta	30	39	Aves	Passeriformes	Meliphagidae	10	64
Lophophaps ferruginea	33	39	Aves	Columbiformes	Columbidae	80.7	66
Meliphaga virescens	34	39	Aves	Passeriformes	Meliphagidae	27.5	64
Passer domesticus	25	28	Aves	Passeriformes	Passeridae	23.7	78
Poecile gambeli	14.7	32	Aves	Passeriformes	Paridae	10.95	65
porphyrio hochstetteri	9	31	Aves	Gruiformes	Rallidae	2758.3	75
Porzana cinerea	28	37	Aves	Gruiformes	Rallidae	47.9	75
Ptilinopus melanospila	22	33	Aves	Columbiformes	Columbidae	98.7	71
Ptilinopus perlatus	24	32	Aves	Columbiformes	Columbidae	196	71
Pycnonotus sinensis	25	33	Aves	Passeriformes	Pycnonotidae	29.38	80
Ramphastos dicolorus	20	34	Aves	Piciformes	Ramphastidae	328.9	73
Scardafella inca night	32	35	Aves	Columbiformes	Columbidae	42	61
Sporophila aurita	28.9	39.2	Aves	Passeriformes	Emberizidae	9.8	60
Thinocorus rumicivorus	33	38	Aves	Charadriiformes	Thinocoridae	55.5	68
Zenaidura macroura	30	37.5	Aves	Columbiformes	Columbidae	91.4	63

References corresponding to Dataset S1

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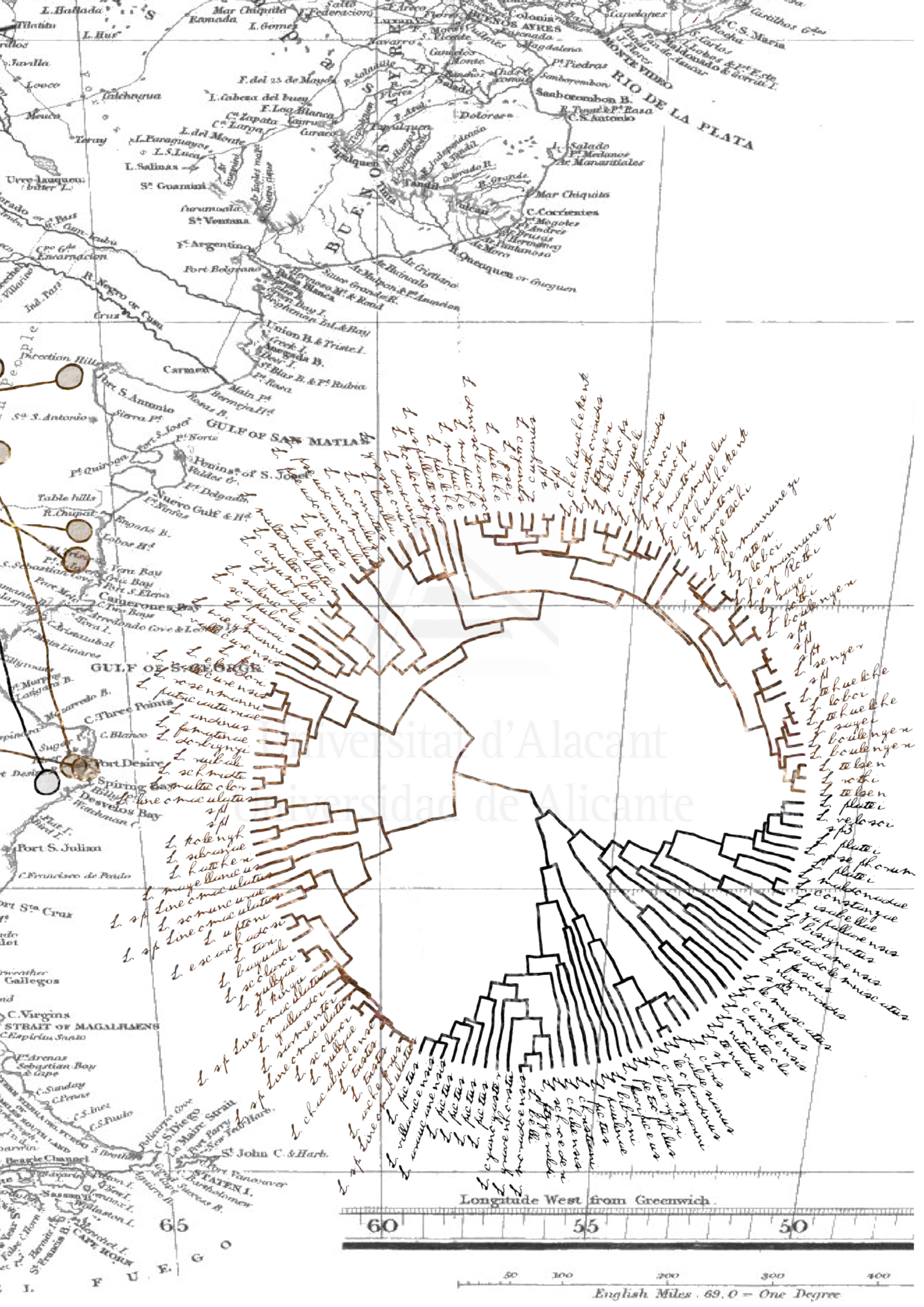
BUENOS AYRES
RIO DE LA PLATA
MONTEVIDEO
Salado
Dolores
Tandil
Mar Chiquita
C. Corrientes
Port Belgrano
R. Negro or Cusu
Carmen
Port S. Antonio
GULF OF SAN MATIAS
Penins. of S. Josef
Nuevo Gulf
GULF OF S. GEORGE
C. Three Points
C. Blanco
Port Desire
Desvelos Bay
Port S. Julian
C. Francisco de Paulo
Port Sta Cruz
Gallegos
C. Virgins
STRAIT OF MAGALHAENS
C. Espiritu Santo
C. S. Diego
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St John C. & Harb.
STATEN I.
CAPE HORN
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L. chehuachekenk
L. kingii
L. archeforus
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L. escarchadosi
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L. zullyae
L. sarmientoi
L. uptoni
L. somuncurae
L. sp. lineomaculatus
L. magellanicus
L. hatcheri
L. silvanae
L. kolengh
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L. morenoi
L. dorbignyi
L. fitzgeraldi
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L. sagei
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L. cuyanus
L. josephorum
L. darwinii
L. pictus
L. chiliensis
L. tenuis
L. lemniscatus
L. fuscus
L. nigroviridis
L. bisignatus
L. isabelae
L. constanzae
L. velosoi
L. platei
L. zapallarensis
L. pseudolemniscatus
L. monticola
L. nitidus
L. curicensis
L. confusus
L. villaricensis
L. cyanogaster
L. gravenhorstii
L. buergeri
L. petrophilus
L. quilmes
L. elongatus
L. cristiani
L. chacabucoense
L. sp
L. sp3

Chapter II

Capítulo II

Diversification patterns and historical biogeography of the genus *Liolaemus*

INTRODUCTION

Iguanid lizards constitute one of the most diverse groups of reptiles, harboring two of the most species-rich genera of lizards on Earth: *Anolis* and *Liolaemus*. These two genera represent a classic example of adaptive radiations, with species showing a wealth of morphological, ecological and physiological adaptations (Schulte et al. 2000, 2004, Losos 2009, Pincheira-Donoso et al. 2015).

The family Liolaemidae comprises around 290 described species unevenly distributed in three genera *Ctenoblepharys*, *Liolaemus* and *Phymaturus*, and is distributed in South America from central Perú to Tierra del Fuego in Chile and Argentina (Quinteros 2012). While *Ctenoblepharys* is represented by a single species from the coastal desert of central (Perú), and there are 42 species of *Phymaturus* occurring only in the Patagonian and Andean regions of Argentina and Chile, the genus *Liolaemus* comprises 240 species and it is widely distributed across ca. 4500 km of latitude from Central Peru to Tierra del Fuego. Across this range, the diversity of *Liolaemus* lizards is present in a wide variety of habitats and climates, from desert regions like the Atacama Desert, to austral temperate and subtropical forests, mediterranean scrub, coastal dunes, alpine environments in the Andes, or the Patagonian landscapes, showing an altitudinal range from sea level to ca. 5000 m a.s.l. (Labra et al. 2009). This extensive environmental and geographic distribution is associated to the evolution of highly diverse phenotypes (i.e. morphology, coloration), ecologies, physiological tolerances and life-history adaptations (e.g. Espinoza et al. 2004, Pincheira-Donoso et al. 2008, 2011, Tulli et al. 2011), with viviparism appearing in multiples occasions (Schulte et al. 2000, Pincheira-Donoso et al. 2008b) as an adaptation to colder environments.

The phylogenetic relationships of liolaemids have been extensively studied (e.g. Schulte et al. 2000, 2003, Morando et al. 2003, 2004, Avila et al. 2004, 2006, Victoriano et al. 2008, Schulte II and Cartwright 2009, Fontanella et al. 2012, Medina et al. 2014, Olave et al. 2014). Their phylogenic position within iguanids has been clarified with a phylogenomic study (Townsend et al. 2011 but see Okajima and Kumazawa 2009), that shows that they are the sister taxon to a clade formed by South American Leiosauridae and Malagasy Opluridae. Within *Liolaemus*, earlier works based on mitochondrial DNA recovered two main clades corresponding to two subgenera: *Liolaemus sensu stricto* and *Eulaemus* (Schulte et al. 2000), which was later confirmed by including multiple nuclear loci (Fontanella et al. 2012, Olave et al. 2014). The relationships at the species level have been mainly investigated using mitochondrial DNA (Schulte et al. 2000), which was not enough to resolve most relationships, but identified several clades including: *Liolaemus nigromaculatus* group, *L. lemniscatus* group, *L. elongatus*-*L. kriegii* complexes, *L. bibronii*-*L. alticolor* groups, *L. chiliensis* group, *L. lineomaculatus* section, *L. montanus* series, *L. wiegmannii* series, *L. melanops* group, and *L. darwinii* complex. The incorporation of multiple nuclear loci improved phylogenetic reconstructions, but still suffered from short branching that suggests a rapid diversification within the *Eulaemus* clade which is difficult to resolve (Olave et al. 2014). So far, we lack a multi-locus analysis including both subgenera to try to better outline the phylogenetic relationships within liolaemids and which would serve as a base for the reconstruction of the diversification pattern and historical biogeography of this clade.

Considering the current distribution of *Liolaemus*, the evolution and diversification within this clade may have been linked to the uplift and orogeny of the Andes (Cei 1993, Schulte et al. 2000, Fontanella et al. 2012). Gregory-Wodzicki 2000 reviewed the quantitative paleoelevation estimates for the central Andes based on paleobotanical and geomorphological evidence and concluded the Altiplano-Puna reached no more than a third of its modern elevation by 20 milion years ago (mya) and no more than half its modern elevation by 10.7 mya, therefore, the Andean uplift would have begun in early Oligocene becoming more pronounced at early Miocene and mid Miocene (19-25 mya and 11 mya) continuing until present day (Gregory-Wodzicki 2000). Other recent reconstructions based on leaf morphology (Gregory-Wodzicki 2002), carbonate clumped isotope thermometry (Ghosh et al. 2006) and carbonate oxygen isotopic compositions (Garzione et al. 2006) suggested a more recent and rapid rise of the Andes during the late Miocene. This late and rapid uplift is, nevertheless, in disagreement with geomorphological data that indicates a slower uplift starting at about 40 mya in late Oligocene (Sempere et al. 2006, Hartley et al. 2007, Barnes and Ehlers 2009, Mamani et al. 2010). Barnes and Ehlers 2009 compared evidences for a rapid uplift since 10mya and for a slow-steady uplift since 40 mya concluding that evidence favours the later. Also, Poulsen et al. 2010 concluded that the observed pattern of $\delta^{18}O$ is not only explained by uplift of the central Andes but also due to climatic effects suggesting that the levels of $\delta^{18}O$ in Miocene carbonates and interpreted as sea level are consistent to an altitude of 2000 masl. Nevertheless Leier et al. 2013 used new carbon and oxygen isotope data as evidence of multiple pulses of rapid surface uplift in central Andes and Winton et al. 2013 used deuterium isotopes from Miocene volcanic glass that supports a non uniform uplift of the Andes. More recently, Fiorella et al. 2015 quantified the relation between central Andean precipitation and surface waters by measuring the isotopic composition ($\delta^{18}O$ and δD) of surface waters. Accounting for the effect of paleoclimates they proposed Altiplano paleoelevations of 1-2 km at 24.5 mya, 1.5-2.9 km by 11.45 mya and reach modern elevations by 6 mya, constraining the total uplift between late Miocene to present to less than 2.2 km, which is more consistent with crustal shortening records.

In any case, this affected the climate in both slopes, resulting in one of the strongest rain-shadow effects worldwide which supposed strong ecological changes in both slopes (Blisniuk et al. 2005, Poulsen et al. 2010, Hoorn et al. 2010).

Using mitochondrial DNA and a fixed mutation rate Schulte et al. 2000 estimated the divergence between *Liolaemus* and *Eulaemus* around 12.6 mya, coinciding with the Miocene uplift acceleration of the Andes proposed in the rapid Miocene Andean uplift model by Gregory-Wodzicki 2002, and interpreted this as a vicariant event that separated both subgenera followed by several events of dispersal and vicariance of species between the eastern and western slopes and the Andes. A recent study, using a single fossil calibration and incorporating nuclear data suggests older ages (Fontanella et al. 2012), with an initial divergence in *Eulaemus* around 18 mya, but not providing the age of the split between subgenera which should be older. Pincheira-Donoso et al. 2015 used the midpoint between the molecular estimation from Fontanella et al. 2012 and the paleontological evidence from Albino 2011, placing the *Liolaemus*-*Eulaemus* split in ~19 mya. The discrepancies are wider considering the results of another study that used mitochondrial DNA and multiple fossil calibrations to date these lineages, resulting in an age of ca. 47 mya for the split between *Liolaemus* and *Eulaemus*, and crown ages for *Liolaemus* of ca. 36 mya and for *Eulaemus* of ca. 39 mya (Schulte 2013). It has been shown that mitochondrial DNA overestimates divergence times (Ho et al. 2005), but the differences are so large that question previous interpretations about the diversification and historical biogeography of these groups. If the origin and divergences within these clades predate the Miocene uplift of the Andes, this geographic event cannot be invoked to explain phylogenetic splits by Andean vicariance, and other evolutionary and biogeographic scenarios have to be considered.

The estimated ages of the origin of the family are also controversial. (Schulte et al. 2003) recovers the split between Liolaemidae and other iguanids around 135 mya. However, a study with multiple nuclear loci and fossil calibrations recovers this node around 62 mya (Townsend et al. 2011), and the split between Opluridae from Madagascar and Leiosauridae from South America around 55 mya. This is in disagreement with other studies that recovered the South American – Malagasy split around 90 mya in the mid Cretaceous (Noonan and Chippindale 2006, Crottini et al. 2012), that do not support the previously hypothesized Late Cretaceous connections of Madagascar and South America via Antarctica and the Kerguelen/Gunnerus ridges (Noonan and Chippindale 2006, Ali and Aitchison 2009, Ali and Krause 2011), and directly imply that the node Liolaemidae-other iguanids should be older than 90 mya.

Considering that *Liolaemus* has undergone an enormous diversification, and that dramatic changes in geological and environmental settings happened in the region like the Miocene uplift of the Andes and its consequent climatic change, we can expect a case of adaptive radiation driven by ecological opportunity. Adaptive radiation theory predicts that when a single ancestor is exposed to ecological opportunity by the emergence of new habitats (such as the colonization of an island), environmental changes (e.g., a climate change) or emptying of niches through extinctions, an early burst of diversification would be produced followed by an asymptotic decrease in diversification as new niches are filled and ecological opportunity fades (Pincheira-Donoso et al. 2015). However, contrary to events like island colonization, orogenenetic and associated climate changes are generally gradual processes that span along millions of years, so ecological opportunity (through the arising of new niches) should also be gradual. Therefore an early burst is not necessarily a reasonable expectation for an adaptive radiation (Pincheira-Donoso et al. 2015). Instead, shifts in diversification rate starting at the beginning of the environmental change and lasting for the duration of it is a more reasonable expectation. On the other hand, other processes of diversification with none or little adaptation can also shape the diversity patterns of *Liolaemus* lizards. Andean orogeny has not only created new habitats which can promote adaptive radiations but also new barriers which solely or in combination with climatic changes and fluctuations can produce isolation of populations resulting in multiple allopatric speciation events.

Here, we assembled the largest nuclear and mitochondrial dataset for Liolaemidae so far, by expanding the subgenus *Eulaemus* dataset of (Olave et al. 2014) including 79 samples from 43 more species representing the diversity of the subgenus *Liolaemus*, across most of the range of the family. We used this dataset to infer the phylogeny of the whole genus with large species coverage. We then used this phylogenetic hypothesis to estimate divergence times and perform analyses to test different hypotheses, including a) infer lineage diversification through time to test whether there where bursts of speciation in particular periods of time, related to climatic or geological events, or if lineages accumulated continuously though time; b) assess for different patterns of diversification within clades of the phylogeny of *Liolaemus* and c) assess if diversification patterns are related to climatic or geological changes in the region, if the estimated ages for the main lineages are congruent with the hypothesis of Miocene diversification in parallel to the Andean uplift, or whether the basal diversification predated the uplift of the Andes and this geological event shaped more recent nodes. With those data we reconstruct the biogeographic history of the clade and clarify the potential barrier effect and permeability to dispersal of the Andes through time.

MATERIALS AND METHODS

TAXON SAMPLING

We collected specimens in the field across a wide latitudinal gradient covering most of the Chilean range of the family Liolaemidae. Whenever possible, we collected specimens from type localities. Specimens were collected by hand or noose, sacrificed by intraperitoneal injection of lidocain at 1% dissected slightly to extract a sample of liver/muscle for molecular study, and fixed in 70% ethanol. Tissue samples were divided and stored both on part in 99% Ethanol and another part frozen in -80 ºC. Voucher specimens are deposited in the herpetological collection of the Pontificia Universidad Católica de Chile in Santiago de Chile (Voucher information is summarized in Table S1).

We included several representatives of the genus *Phymaturus*, as well as other iguanids as outgroups. Our dataset covers 157 species, supposing a 54% of the whole diversity of the family, covering the main lineages within the genus *Liolaemus*. The samples included are distributed across most of the full distribution of the family Liolaemidae.

DATA COLLECTION

Genomic DNA was extracted from tissue samples, frozen or preserved in ethanol, using the Qiagen ® DNeasy ® 96 Tissue Kit (Qiagen, Valencia, CA, USA) following the protocol provided by the manufacturer. Two mitochondrial genes and five protein-coding nuclear genes were amplified and sequenced. We selected a set of loci available for Liolaemid lizards that included both fast-evolving (e.g. mitochondrial DNA) and protein-coding genes with intermediate rates of evolution. We expanded a recently published dataset for the subgenus *Eulaemus* (Olave et al. 2014) including many representatives from the other subgenus as well as *Phymaturus* and other iguanid outgroups. A sample of *Ctenoblepharys* was not available to us so we could not include all liolaemid genera.

Loci amplified included the mitochondrial 12S rRNA and Cytochrome B, using primers from Troncoso-Palacios et al. (2015) (Table S1). Novel primers were developed for five nuclear markers that amplify well across all the diversity of *Liolaemus* and are summarized in Table 1. 401 base pairs (bp) of the serine/threonine-protein kinase mos gene (C-MOS) were amplified with the primers LIO_DRV_CMOS_F and LIO_DRV_CMOS_R. 782 bp of the matrix-remodelling associated 5 protein (MXRA5) were amplified with the primers LIO_DRV_MXRA5_F and LIO_DRV_MXRA5_R. 506 bp of the Kinesin family member 24 protein (KIF24) were amplified with the primers LIO_DRV_KIF24_F and LIO_DRV_KIF24_R. 967 bp of the Pinin desmosome associated protein (PNN) were amplified with primers LIO_DRV_PNN_F and LIO_DRV_PNN_R. 490 bp of Prolactin receptor (PRLR) were amplified with primers LIO_DRV_PRLR_F and LIO_DRV_PRLR_R.

Fragment length varied among taxa due to missing nucleotides at the beginning of the sequences and different lengths of variable regions, corresponding to loops in the secondary structure of the 12S rRNA molecule and insertions/deletions in nuclear loci. Although the different loci have different predicted melting temperatures, a test using a gradient PCR showed that all work well at an annealing temperature of 51, hence we used the same PCR protocol for all loci and samples. PCRs were performed using the following conditions: an initial denaturation at 94 °C for 2 min, 39 cycles at 94 °C for 30 sec, annealing at 51°C for 30 sec, extension at 72 °C for 2 min; and a final extension of 5 min at 72 °C. PCR products were loaded onto 1% agarose gels, stained with GelStar gel stain (Cambrex), and visualized in a Dark reader transilluminator (Clare Chemical). Products were then purified using 2 μL, from a 1:4 dilution of ExoSapIt (Amersham) per 2 μL of PCR product prior to cycle sequencing. A 10 μL sequencing reaction included 2 μL of template, 2.5 μL of sequencing buffer, 0.8 μL of 10 pmol primer, 0.4 μL of BigDye Terminator version 3.1 Sequencing Standard (Applied Biosystems) and 4.2 μL of water. The sequence reaction was 35 cycles of 10 s at 96 °C, 10 s at 50 °C and 4 min at 60 °C. Cycle sequencing products were purified by a pipetting robot. Sequence data collection and visualization were performed on an ABI 3730xl automated sequencer (Applied Biosystems). Sequences are deposited in GenBank (*accession numbers to be added upon manuscript acceptance*).

Sequences were automatically aligned using the computer program Muscle (Edgar 2004) clustal X under the default parameters, and the alignments were adjusted manually considering amino acid properties. Several ambiguous regions of the 12s rRNA gene were excluded from analyses, as well insertions and deletions in nuclear loci where more than 20% of the samples lacked them. We performed phylogenetic analyses for the complete dataset including all nuclear and mitochondrial markers.

PHYLOGENETIC ANALYSES

Phylogenies were inferred by both a maximum likelihood and a Bayesian approach. Because of the saturation of the third codon position of the cytochrome b locus, we performed analyses including and excluding this position. Non-parametric bootstrap maximum likelihood analysis was performed with the program RaxML version 8 (Stamatakis 2014). One thousand bootstrap repetitions were run for each dataset twice to test for congruence on the most likely tree, and a 50% majority rule consensus tree was calculated. Bayesian inference of phylogeny was performed with both the unpartitioned dataset and a partition strategy by codon and gene. Separate evolutionary models and parameters that best fit each partition were selected for the first, second and third codon positions of each protein-coding gene and for the complete 12S rRNA using PartitionFinder (Lanfear et al, 2012). The most suitable model for mitochondrial genes was GTR+I+G; for CMOS was HKY+I; for KIF24, MXMRA5 and PRLR was HKY+G, and for the PNN the best model selected was HKY+I+G. These model parameters were used as priors in the Bayesian analyses in the program MrBayes, version 3.2.3 (Ronquist and Huelsenbeck, 2003). Analyses were performed under different partitioning strategies. They included three partition schemes: unpartitioned dataset, partition by gene only, partition by codon and gene. For each partition strategy, we ran two independent analyses consisting of four Markov chains that ran for 40 million generations, sampled every 1000 generations, with a random starting tree, default priors, and the option "*prset ratepr*" set as "variable" to ensure that branch lengths were estimated separately for each partition. The temperature was optimized between 0.03 and 0.05 after several preliminary test runs for one million generations for each dataset. Stationarity and convergence between runs was assessed using the "*sump*" command in MrBayes, and with trace plots generated in TRACER V1.4 (Rambaut and Drummond, 2007). Most runs became stationary after 10 to 15 million generations, so after discarding the first 20 million generations, the remaining trees from both analyses for each dataset were combined and a 50% majority rule consensus tree was calculated. In order to assess which partition strategy performed better, we employed Bayes factors (Huelsenbeck and Imennov, 2002).

DIVERGENCE TIME ANALYSES

There are not many available fossils of Liolaemids, and most of them are from the Pleistocene but a fossil from the Southern Cliff of lower Chubut River Valley near Gaiman, Chubut Province in Argentina, was dated from the Burdigalian-Aquitanian (16-23 mya) and assigned to *Liolaemus* (Albino 2008, 2011). This fossil has been placed in the subgenus *Eulaemus* and used as a single calibration constraint to date the minimum age for the split between *Eulaemus* and *Liolaemus* (Fontanella et al. 2012). Hence, in order to maximize the amount of taxa used as calibration constraints, we followed a mixed strategy for divergence time reconstruction. We gathered data from other clades outside liolaemids. As most candidate taxa available in Genbank for potential calibration constraints lacked some of the loci sequenced by us, and because mitochondrial markers are saturated at deep phylogenetic scales, hence they are not suitable for estimating divergence time in old branches, we ran a first divergence time analyses with three nuclear loci only (CMOS, PNN and PRLR). By using those, we were able to include multiple calibration constraints using a set of three conserved nuclear markers available for most taxa. Then, we used the divergence times obtained in the first analysis for liolaemid nodes, using *Anolis* as outgroup, to run a second divergence times analysis including all loci and all liolaemid species to get a timetree for all of them.

We explored the use of the program BEAST version 1.8 (Drummond et al. 2012) for divergence-time estimations using the Bayesian uncorrelated lognormal approach. We did preliminary tests with a fully partitioned dataset by codon and gene, but this strategy did not provide high effective sample size (ESS) values for some values despite long runs, hence we ran analyses with a partition by gene. Despite several long runs, the analyses did not converge and ESS values were not high, mainly because the dataset is very large. Hence, we changed the strategy and used a recent software for divergence time estimations for large genomic datasets called RelTime (Tamura et al. 2012) and implemented in MEGA7 (Kumar et al. 2016). A recent study did not found significant differences in divergence time estimates between BEAST and RelTime results (Chriki-Adeeb and Chriki 2016), suggesting that results are at least comparable between methods. RelTime uses a maximum likelihood approach to produce divergence times without selecting statistical distribution models as priors to model rate heterogeneity among branches. It also does not need a deep knowledge of prior divergence times. We used as input tree the most likely tree recovered in our RaxML analysis, and several calibration constraints based on the fossil record. Those constraints included the following: the split between *Xenosaurus* and *Elgaria* dated with a minimum age of 99 mya, (Hugall et al. 2007); the split between *Varanus* and *Shinisaurus* is older than 85 mya (Hugall et al. 2007); the most recent common ancestor of Iguania and Anguimorpha dated on 144 mya based on the fossil anguimorph *Parviraptor estesi* (Rieppel 1994); the split between Rhynchocephalia and Squamata corresponding to the earliest identified rhynchocephalian dated in 227 mya (Sues and Olsen 1990); the most recent common ancestor of Teiidae + Gymnophthalmidae with a minimum age of 99 mya based on the fossil teiid, *Bicuspidon* (Nydam and Cifelli 2002); the most recent common ancestor of *Amphisbaenia* and Lacertidae based on the fossil amphisbaenian *Hodzhhakulia* from the middle Cretaceous with a minimum age of 98 mya (Gao 1997); the most recent common ancestor of *Agkistrodon* (Viperidae) and *Lampropeltis* (Colubridae) based on the fossil pythonid, *Pachyrachis* from the Cenomanian, with a minimum age of 93.5 mya (Zaher and Rieppel 2002); the most recent common ancestor of Cordylidae and Xantusiidae based on various fossil scincid genera from the Upper Cretaceous, with a minimum age of 65 mya (Carroll 1988); the most recent common ancestor of Varanidae + *Lanthanotus* 65 based on the fossil varanid, *Palaeosaniwa* from the Upper Cretaceous (Balsai, Michael J. 2001); the most recent common ancestor of Rhineuridae and the remaining amphisbaenians based on the fossil rhineurid *Plesiorhineura* from the Torrejonian, with a minimum age of 60.5 mya (Sullivan 1985); the split between *Sceloporus* and *Crotaphytus*, based on the first fossil occurrence of *Leiocephalus* from the Orellan (Cenozoic) of Wyoming, being older than 32.3 mya (Setoguchi 1978, Holman and Sullivan 1981); the age of Iguania can be constrained between the earliest definitive pleurodont iguanian (*Armandisaurus*) with affinities to extant taxa from the early Miocene, (Norell and de Queiroz 1991, minimum age of 25 mya), and the assumption that the origin of this clade does not predate the earliest-known iguanian in the Jurassic (Evans et al. 2002, maximum age 180 mya); the split between *Exiliboa* and *Charina*, with a minimum age of 55 mya (Rage 1994) based on *Dunnophis* from the Eocene (Albino 1996); the minimum age of Boinae 55 mya based on *Cheilophis* from the Eocene (Albino 1993, 1996, Rage 1994); the minimum age of Boidae based on *Dinilysia* from the

Cretaceous (Rage 1994); the split between Acrodont and Pleurodont iguanians based on the early-middle Jurassic *Bharatagama* from India, which provides a minimum age of 165 mya (Evans et al. 2002), while the maximum age should be the iguanian-scleroglossan dichotomy that extends back into the early Jurassic or even Late Triassic (maximum age of 230 mya, Evans et al. 2002); the split between *Agkistrodon* (Viperidae) and *Epicrates* (boinae) based on the fossil pythonid *Pachyrachis* from the Cenomanian, with a minimum age of 93,5 mya (Zaher and Rieppel 2002); the split between *Anilius* and *Tropidophis*, based on the Cretaceous Coniophis (Rage 1994) with a minimum age of 75 mya; the split between Crocodilia and Rhynchocephalia constrained between 263 mya and 304 mya; and the split between Iguanidae and Tropiduridae based on Polychrus from the Chadronian, with a minimum age of 44 mya (Pearson and Hoganson 1995, Smith 2006). For the analysis of diversification rates and the effect of the environment on diversification we pruned the dataset leaving only one tip per species in any monophyletic group composed of samples of the same species.

DIVERSIFICATION RATES

To test for the early burst of diversification we performed a Monte Carlo Constant Rate (MCCR) test (Pybus and Harvey 2000). The lambda statistic compares the distributions of inter node distances between the tree root and the tips to the temporal midpoint, when λ is negative internode distances between the root and the midpoint are shorter than between midpoint and the tips, which is indicative of an early burst of diversification. The MCCR test simulates incompletely sampled phylogenies and calculates the γ statistic approximating the expected distribution of γ values expected under constant diversification. This allows to estimate the value below which true γ is significantly smaller than expected by change and, therefore, an early diversification pattern. We also plotted the temporal variation in diversification rates using semi-logarithmic lineage-through-time (LTT) plot. We used packages Geiger, Laser and Phytools in R version 3.2.4 (2016-03-10) to perform these analyses.

Based on spectral graph theory, Lewitus and Morlon (2015) have developed a methodology for the systematic characterization and comparison of all the information contained in the shapes of phylogenies. This also allows to identifying distinct modes of division (branching patterns) within a tree. The method treats the tree as a graph composed of nodes (N) representing species, edges (E) representing the relationships between nodes and a weight function (w) that define the distances between species. The approach begins constructing a Modified Graph Laplacian (MGL) of the phylogenetic tree (the difference between its degree matrix, which is the diagonal matrix where diagonal element *i* is the sum of all distances from node *i* to all other nodes, and its distance matrix, where the element (*i*,*j*) is the negative of the branch-length between nodes *i* and *j*. Each row and column, therefore sums up to zero). As the MGL is a positive matrix, it has *N* non-negative eigenvalues $\lambda_1 \geq \lambda_2 \geq \ldots \geq \lambda_{N-1} \geq \lambda_N \geq 0$. Each of those eigenvalues represents the connectivity of the tree in a region of the tree. To represent the whole organization of the tree a density profile of spectrum of eigenvalues (the spectral density profile) is created by convoluting λ with a smoothing Gaussian Kernel function. The spectral density is then plotted as a function of ln(λ) and $f(x)=(f(x))/(\int f(y)dy)$. Larger λ represent sparser nodes separated by longer branches and vice versa. Skewness and kurtosis can be then computed providing information on the relative abundance and distribution of λ. To identify modalities within the phylogeny (regions of the tree with different shape, indicating different diversification patterns), λ are computed from the MGL and ranked in descending order, the position of the largest gap between two consecutive λ (the eigengap) is indicative of the number of clusters in the phylogeny (Shen and Cheng 2010); also, the number of peaks in the spectral density profiles are indicative of different clusters in the phylogeny. Those clusters could be composed of non-adjacent branches in the tree. Given the number of modalities, those clusters can be identified in the tree by using k-medoids clustering setting $k = i$ (being i the number of clusters). Confidence intervals can then be obtained for those modalities by comparing BIC values detecting the modalities in the tree with those of randomly bifurcating trees (Dan Pelleg 2000).

EFFECT OF THE ENVIRONMENT ON DIVERSIFICATION OF *LIOLAEMUS*

To quantify the effect Andean uplift and global temperature change had on diversification we use the methods proposed by Morlon et al. (2011) and Condamine et al. (2013) and implemented in the package RPANDA in R 3.2.3 (R Core Team 2013, Morlon et al. 2015). This method builds time dependent diversification (birth-death) models and also allow speciation and extinction rates to depend not only on time but also on an external time-dependent variable.

The model assumes that the clade has evolved following a birth-death process with speciation (λ) and extinction (μ) rates that can also vary through time and can be influenced by one or several time varying environmental variables. The method can take into account extant species not included in the phylogeny by assuming that each species has a probability of being sampled ≤ 1. The probability density of observing such a phylogeny is adapted from Morlon et al (2011). Those expressions can be used to derive likelihoods for any functional form of λ and μ (such as constant, linear or exponential), parameterized by a set of X parameters.

The model requires to specify the assumed functional form of the environmental dependency and uses as arguments a time calibrated phylogeny, a time dependent environmental variable, a set of initial parameter values, the fraction of extant species included in the phylogeny and the functional dependence function for λ and μ. The model returns the parameter estimates for λ and μ (the speciation/extinction rates at present and the rate of change of speciation/extinction) as well as the maximum log-likelihood value and the corrected Akaike Information Criterion (AICc). We fit time dependent models and environmental dependent models using linear and exponential functional forms for λ and μ and compare the log-likelihood and the AICc if the environmental variables (global temperature and Andean uplift) perform better than the time dependent models.

We fitted time-environmental diversification models for four different conditions for each variable: assuming a linear or an exponential relation between diversification and the environmental variable and time; and considering the crown age of the phylogeny (the age of the oldest internal split of the phylogeny) or the stem age (the age of the split between the group of interest (*Liolaemus*) and its sister taxa (*Phymaturus*). We therefore created four different models for each variable and used AICc to compare their performance. We also used the same approach for the two subgenera, fitting time-environmental diversification models separately.

We also fitted time-diversification models (excluding the environmental variables) for the same conditions as the time-environmental diversification models to compare the AICc values of the models with or without taken the environment into account. We considered that a model could be considered better than the other when AICc was, at least, two units lower (ΔAICc) (Burnham and Anderson 2004).

ENVIRONMENTAL DATA

Global temperatures from Paleogene to present were obtained from relative proportions of oxygen isotopes ($\Delta^{18}O$) from benthonic foraminifer shell samples based on records from Deep Sea Drilling Project and Ocean Drilling Program (Zachos et al. 2001) sites updated with high-resolution records for the interval spanning the middle Eocene to the middle Miocene in Zachos et al. 2008. These data was converted to absolute temperatures using the formula: $T = 16.5 - 4.3 * \Delta^{18}O + 0.14 * (\Delta^{18}O)^2$ (Epstein and Mayeda 1953, Condamine et al. 2013).

Paleoelevation data was estimated from Fiorella et al. (2015). These authors reanalyzed and reinterpreted evidence of historical uplift of central Andes based on isotopic composition of paedogenic carbonates ($\delta^{18}O_{cc}$) and found that paleoarchives underestimated neogene elevations in the Altiplano and Eastern cordillera, improving the match between reconstructed paleoelevation and cumulative shortening percentage. We used the software DataThief® to retrieve the upper and lower bounds of the range of altitudes through time suggested in Fiorella et al (2015) for the Bolivian Altiplano. We estimated the average uplift path by calculating the mean from those upper and lower limits. We also fitted models with the upper and lower limits of the uplift estimation from Fiorella et al. (2015).

Crustal shortening –the reduction in size of the land area of the Earth's crust due to tectonic influences such as collisions with other landmasses, resulting in mountain building (orogeny)– is the is the main cause of the rise of the Andes (Dewey and Bird 1970, Isacks 1988, Sheffels 1990, Dewey and Lamb 1992, Baby et al. 1992, Richard W. Allmendinger et al. 1997). The distribution of shortening has been summarized systematically by Kley and Monaldi 1998. The magnitude of shortening, structures, and timing of deformation has been jointly evaluated with higher resolution for selected transects (Jordan et al. 1993, Echavarria et al. 2003, Ramos et al. 2004, Elger et al. 2005).

RESULTS

DIVERGENCE TIME ANALYSES

The RelTime time-tree places the split between *Liolaemus* and its sister group *Phymaturus* around 57 mya, and the *Liolaemus-Eulaemus* split in 27 mya (Figure 1). Also, the split between the Argentinian *Liolaemus* sensu stricto and their Chilean counterparts is dated around 11 mya for the *L. petrophylus* and *leopardinus* group split and 13 mya. for the *L. bibroni* and *L. paulinae* split (Figura S1).

DIVERSIFICATION RATES

Gamma statistic and MCCR test

The calculated gamma statistic was 1.22, which is indicative of diversification at younger ages. The Monte Carlo Constant Rate Test with 1000 repetitions showed a *P*-values of 0.8886535. The phylogeny, therefore shows no signs of early diversification. On the other hand, the semi-logaritmic Lineage Through Time (LTT) plot is consistent with a constant rate of diversification (Figure 2A).

Spectral Density Analysis

The spectral density profile (Figure 3A and Table 1) is moderately positively skewed, suggesting a tippy phylogeny inconsistent with an early burst. The eigengap is located in

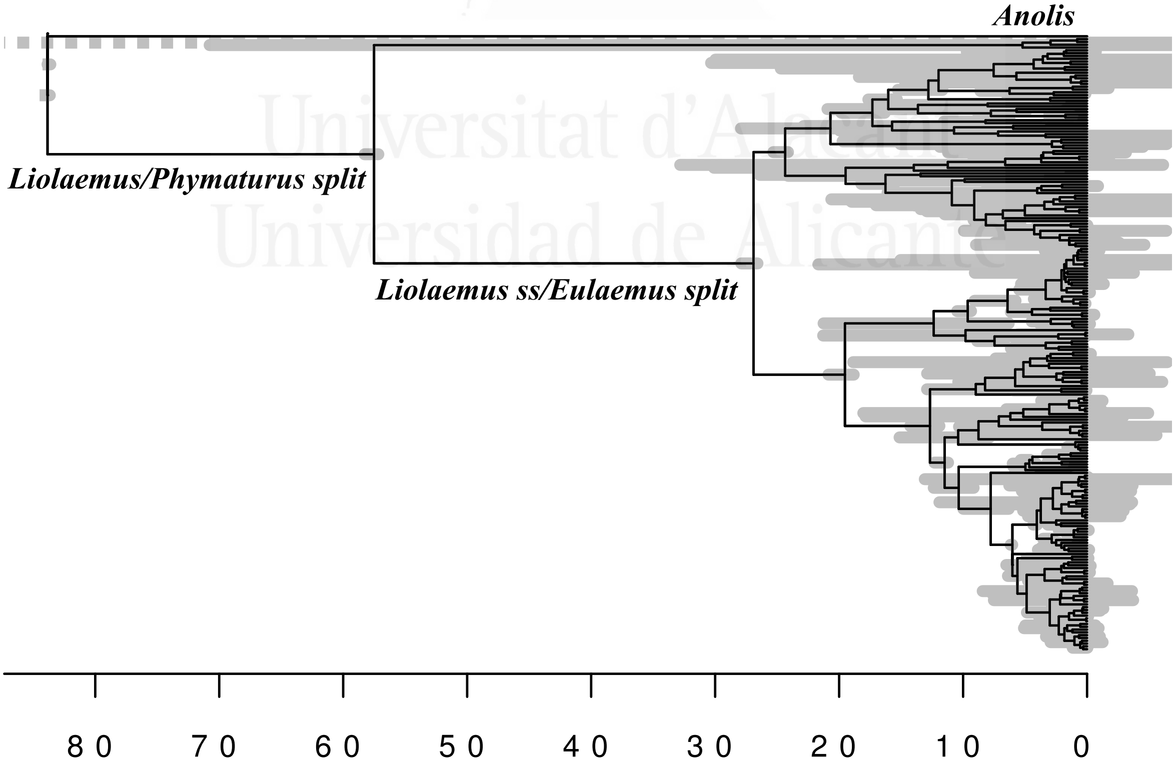

Figure 1. Cronogram of genus *Liolaemus* showing the ages and standard deviation of nodes. Horizontal axis shows the age in millions of years, grey bars show the time confidence intervals of the nodes.

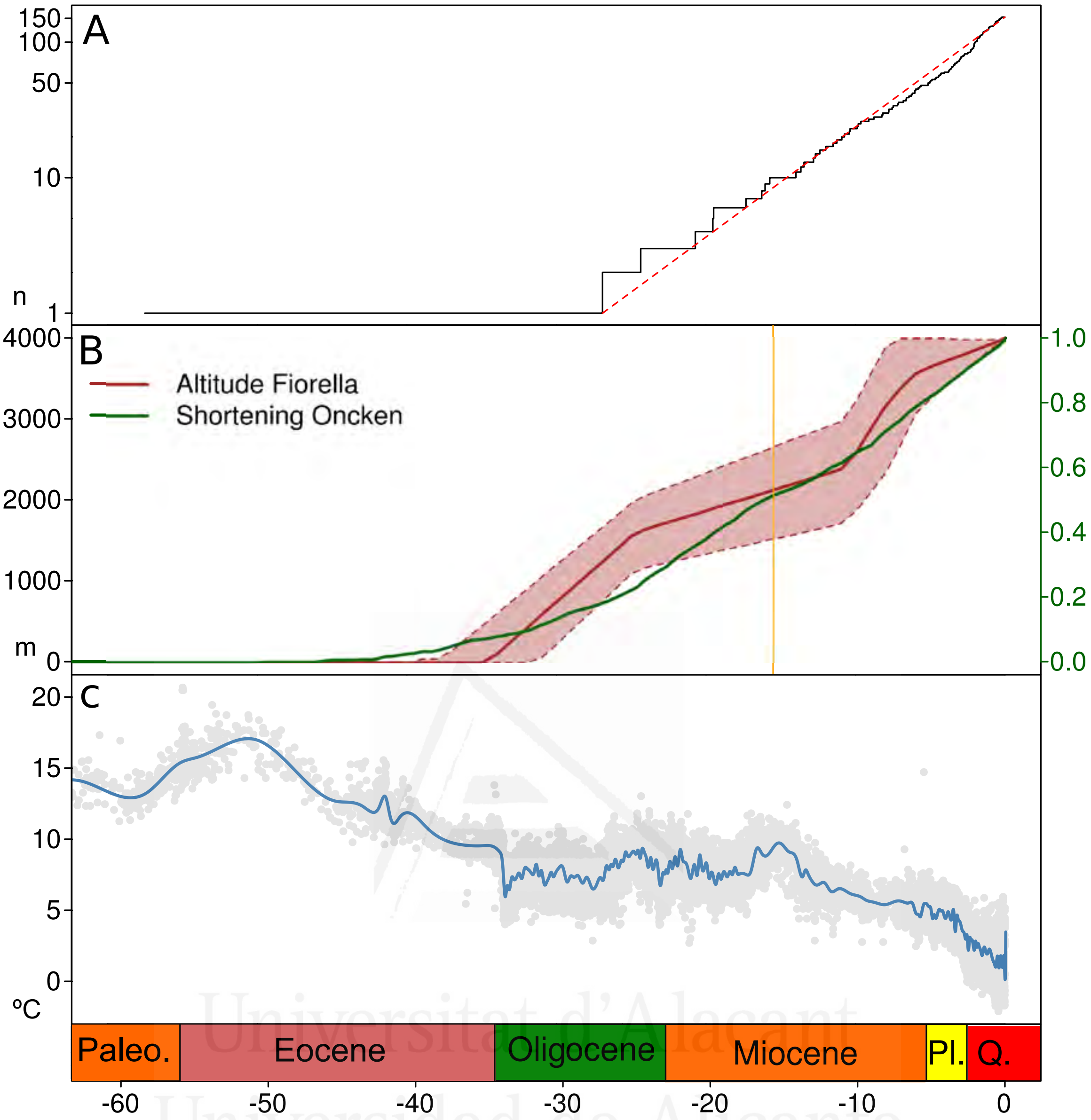

Figure 2. Summary of LTT and the environmental variables used to fit diversification models, the x axis is common for all sub figures and represents time in millions of years. (A) Semi logarithmic lineage-through time plot including lineage stem and crown, y axis represents the logarithm of number of taxa. (B) Crustal shortening from Oncken et. al. 2006 (green) and mean altitude from Fiorella et. al. 2015 (brown) for central Andes. Shaded area represents the range of plausible altitudes from Fiorella et. al. 2015. left axis represents altitude in meters and right axis represents proportion of total shortening. (C) Global temperatures estimated from oxygen isotope rations from Zachos et al. 2008 (light grey). Blue line shows a cubic smoothing spline of the data. Y axis represents temperature in degrees Celsius.

position 1, which is between the first and the second eigenvalues (Figure 3B and Table 1), suggesting a uniform mode of diversification across the different regions of the phylogeny. Nevertheless, the two peaks shown in the spectral density profile (Figure 3A) suggest two different modalities within the tree. We used k-meloids to identify clustering on the phylogeny setting $k = 2$ (Newman 2006). The test significantly distinguished the

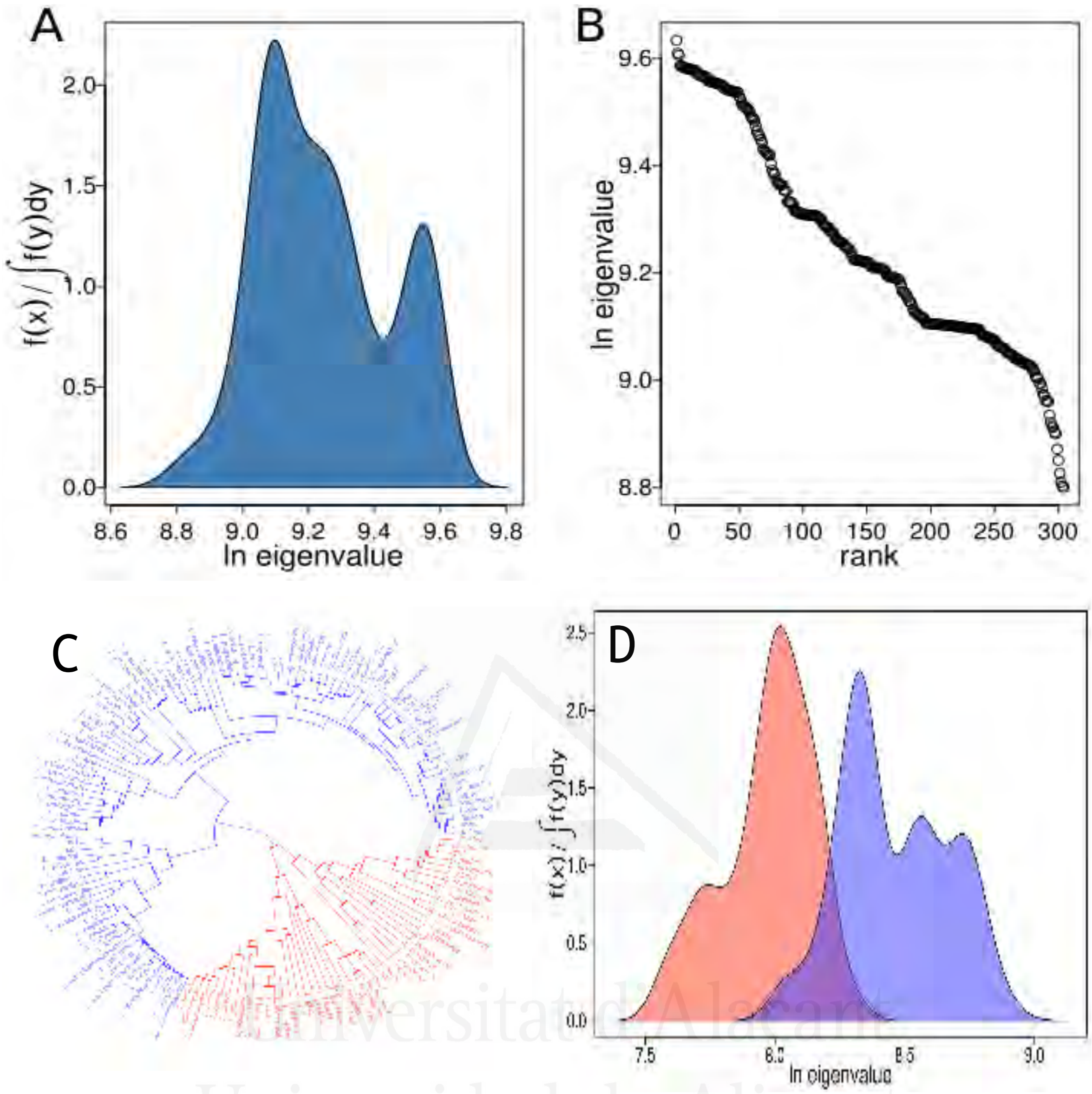

Figure 3. Spectral density profiles of *Liolaemus* and both subgenera. (A) Spectral density profile of *Liolaemus* showing two peaks suggesting two modes of diversification. (B) Ranked logarithm of eigenvalues, showing that the eigengap is in position 1. (C) Distribution of the two clusters along the phylogeny by k-meloifs. Note that the distribution of the clusters did not have to be adjacent, but they match the two subgenera (red: *Liolaemus* s.s., blue: Eulaemus). (D) Spectral density profiles for the two subgenera (red: Liolaemus s.s., Blue: *Eulaemus*). The *Liolaemus* s.s. Profile is left skewed, indicating an early diversification and the *Eulaemus* profile is right skewed, indicative of a late diversification.

two clusters at the 95% confidence interval (tree BIC/random BIC = 5.98761), the two modalities matching the two subgenera (Figure 4C). BSS/TSS ratio was 0.5857117.

We calculated the spectral density profiles for both subgenera. Subgenera *Liolaemus* sensu stricto spectral density profile is left skewed, suggesting an early pattern of diversification while subgenera *Eulaemus* is right skewed, which indicates a later pattern of diversification (Figure 3D and Table 1).

Table 1. Results of the spectral density profile analysis.

	Liolaemus	Sub. *Liolaemus*	Sub. *Eulaemus*
Principal Eigenvalue	15269.21	4076.46	7620.937
Skewness	0.5502499	-0.2556082	0.4722629
kurtosis	2.139394	2.429979	2.20822
largest y-axis value	2.223136	2.537307	2.250877
Eigengap position	1	2	1

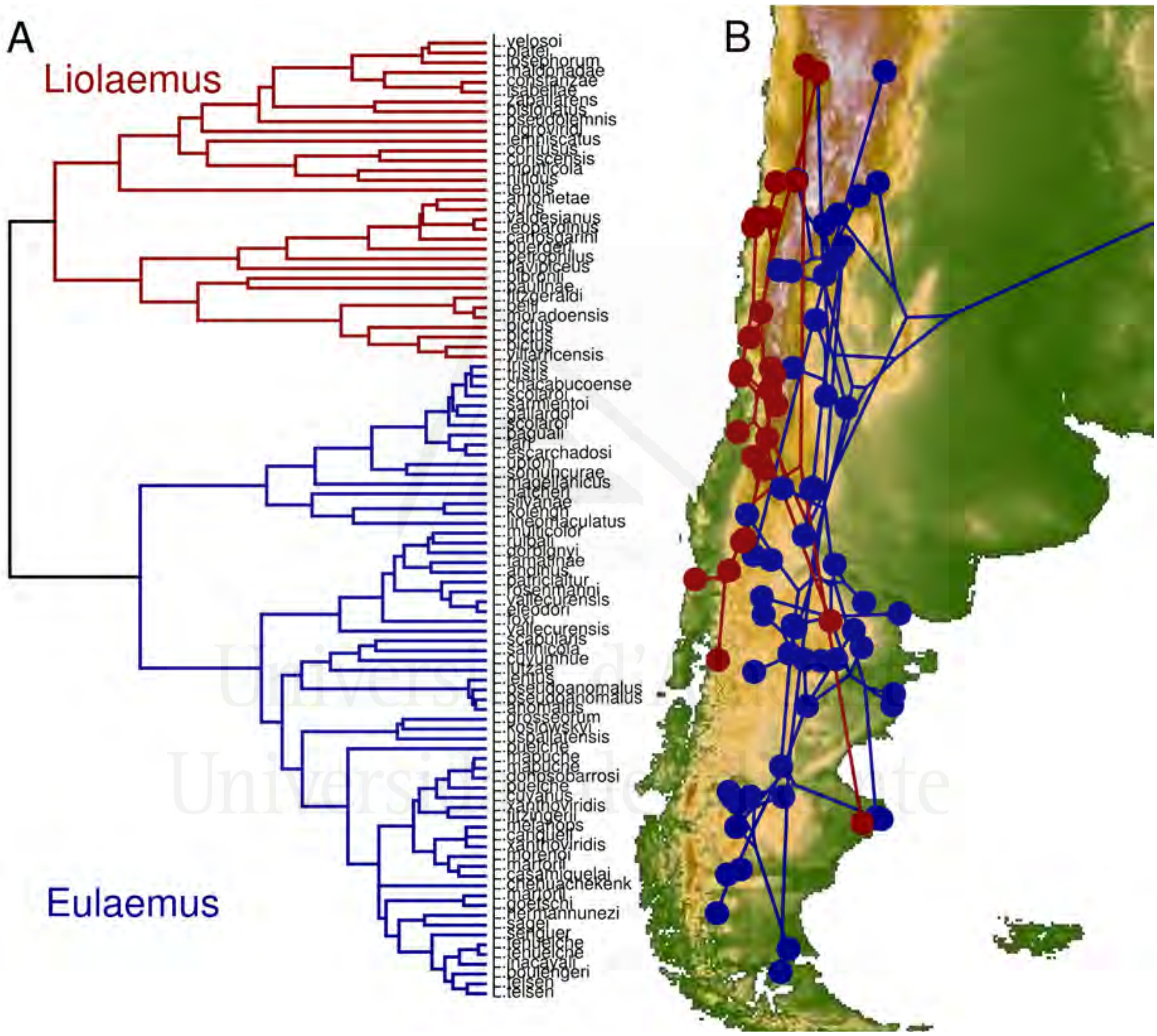

Figure 4. (A) Phylogenetic timetree showing both subgenera and (B) Geographical locations of the samples used in the phylogeny with lines showing their phylogenetic interrelations. Color codes show samples belonging to *Liolaemus* sensu stricto (red) and *Eulaemus* (blue) in both A and B subplots.

Environmental Models

The time-environmental diversification models for the complete phylogeny and for the *Liolaemus* s.s. dataset had similar or higher AICc than the time diversification models (Table 2). On the other hand, the time-environmental diversification models fitted for *Eulaemus*

Table 2. Time-environmental model parameters, Log-likelihood and AICc. Models were fitted using an exponential or a linear function, and using the crown age (the age of the first split within the phylogeny) or the stem age of the phylogeny (the age of the split with its sister group). This creates four kinds of model settings: Models with linear fit and stem age (Linear Stem Models), models with linear fit and crown age (Linear Crown Models), models with exponential fit and stem age (Exponential Stem Models) and models with exponential fit and crown age (Exponential Crown Models). With each of those model settings we fitted models for three variables: global temperature change (from Zachos et al. 2008, Condamine et al. 2013), altitude (from Fiorella et al. 2015) and crustal shortening (from Oncken et al. 2006). Additionally, we also fitted a birth death model (BD model) without any environmental variables, this allows to compare the effect of the variables on the model AICc. λ-par1 and μ-par1 are the speciation/extinction rates at present and λ-par2 and μ-par2 are the rate of change of speciation/extinction)

Linear Stem Models	Variable	Log-Likelihood	AICc	λ-par1	λ-par2	μ-par1	μ-par2
Complete	Temperature	-397.5491	803.3685	0.38293	-0.02511	0.01844	-0.01048
	Altitude	-398.0665	804.4032	6.576E-7	0.00304	0.04511	-0.02162
	Shortening	-397.8249	803.9201	8.39E-7	0.00109	0.01975	-0.00023
	BD model	-394.5542	797.3786	0.23971	-0.00628	-4.300E-6	0.02205
Eulaemus	Temperature	-231.5852	471.5704	0.61813	-0.06311	0.00456	-0.00127
	Altitude	-233.3117	475.0235	-0.18166	0.00630	0.12589	-0.00406
	Shortening	-232.539	473.4781	-0.04163	0.00158	0.22125	-0.00075
	BD model	-200.2203	408.8406	0.44064	-0.01638	-0.23686	0.14034
Liolaemus s.s.	Temperature	-145.9493	300.8289	0.09923	0.01071	0.01107	-0.00453
	Altitude	-146.0734	301.077	0.19908	-0.00065	-0.12198	0.04366
	Shortening	-147.6458	304.2218	0.04998	0.00042	0.00258	-1.404E-5
	BD model	-144.5119	297.954	0.10612	0.00230	3.820E-8	-0.01150

Linear Crown Models	Variable	Log-Likelihood	AICc	λ-par1	λ-par2	μ-par1	μ-par2
Complete	Temperature	-393.6363	795.5428	0.38075	-0.02790	0.01148	-0.00468
	Altitude	-395.2844	798.8391	-0.01231	0.00318	-0.12066	0.13216
	Shortening	-394.4906	797.2514	0.05096	0.00095	0.01020	-0.00032
	BD model	-393.801	795.8723	0.24707	-0.00203	-0.05300	0.06759
Eulaemus	Temperature	-228.8401	**466.0801**	0.51921	-0.03301	0.10756	-0.04050
	Altitude	-230.524	469.448	-0.20749	0.00658	0.31252	-0.29751
	Shortening	-229.6365	467.6731	-0.13593	0.00193	0.23125	-0.00080
	BD model	-230.3534	469.1068	0.36523	-0.01908	-5.677E-9	-0.48990
Liolaemus s.s.	Temperature	-143.7153	296.3609	0.10069	0.01074	0.01654	-0.00677
	Altitude	-146.0734	301.077	0.19908	-0.00065	-0.12198	0.04366
	Shortening	-147.6458	304.2218	0.04998	0.00042	0.00258	-1.404E-5
	BD model	-143.9611	296.8524	0.10137	0.00308	-3.342E-7	-0.01180

Exponential Stem Models	Variable	Log-Likelihood	AICc	λ-par1	λ-par2	μ-par1	μ-par2
Complete	Temperature	-397.2566	802.7835	0.42751	-0.12193	0.00072	0.51177
	Altitude	-397.8817	804.0337	0.06254	0.01656	1.60641	-1.72976
	Shortening	-397.9467	804.1638	0.05803	0.00575	0.37411	-0.15495
	BD model	-394.54	797.3503	0.24281	-0.03170	3.304E-6	0.02662
Eulaemus	Temperature	-232.3638	473.1276	0.69507	-0.17643	2.373E-6	-0.47896
	Altitude	-233.421	475.2421	0.04496	0.02385	0.00072	-0.00100
	Shortening	-232.9363	474.2727	0.05322	0.00719	0.00063	-0.00484
	BD model	-231.131	470.6621	0.36999	-0.06596	-3.245E-8	-0.09927
Liolaemus s.s.	Temperature	-145.951	300.8322	0.11361	0.05034	-5.633E-8	-0.07239
	Altitude	-146.0729	301.076	0.20618	-0.00428	0.06155	-0.17281
	Shortening	-146.0223	300.9748	0.21339	-0.00158	-0.08380	-0.48003
	BD model	-144.5137	297.9577	0.10618	0.02022	-4.865E-7	-0.02752

Exponential Crown Models	Variable	Log-Likelihood	AICc	λ-par1	λ-par2	μ-par1	μ-par2
Complete	Temperature	-393.3447	794.9596	0.46264	-0.14391	-4.674E-7	0.08508
	Altitude	-394.6782	797.6267	0.09146	0.01378	0.00486	0.03152
	Shortening	-394.3137	796.8976	0.06269	0.00545	-1.203E-5	-0.00954
	BD model	-394.3349	796.9401	0.24032	-0.02915	1.993E-6	0.02176
Eulaemus	Temperature	-228.8676	**466.1352**	0.57093	-0.11410	0.00654	0.42516
	Altitude	-230.4891	469.3783	0.04934	0.02292	0.10753	-0.02945
	Shortening	-230.128	468.656	0.05068	0.00736	-8.528E-8	0.00524
	BD model	-231.1076	470.6152	0.36460	-0.06059	-3.396E-7	-0.51002
Liolaemus s.s.	Temperature	-143.7528	296.4359	0.11744	0.04238	-5.21E-6	-0.06583
	Altitude	-143.8522	296.6347	0.18608	-0.00304	0.02794	-0.06968
	Shortening	-143.8396	296.6095	0.18740	-0.00105	-0.06483	-0.12180
	BD model	-143.9656	296.8614	0.10176	0.02734	4.959E-10	-0.03305

using the crown age and global temperature have an AICc of 2 or more units lower than the time diversification models.

DISCUSSION

In this manuscript we have shown that *Liolaemus* split from his sister taxa around 57 mya, and started its own diversification around 27 mya. We have also showed that, although overall the genus has diversified continuously, the two subgenera that conform the clade show oposed patterns of diversification. We also showed that global temperatures seem to have influenced the diversification of the *Eulaemus* subgenus.

According to our results, *Liolaemus* splitted from its sister taxa (*Phymaturus*), about 7 mya after the Cretacic/Tertiary (K-T) transition, and did not show signs of diversification until mid Oligocene, about 27 mya when the split between *Liolaemus* s.s. and *Eulaemus* occurred (Figure 4A). Previous authors suggested a later timing for the split; Schulte et al. (2000) sets the split at 12.6 mya and Fontanella et al. (2012) up to 23.07 mya. Our study sets the split even further back, questioning even more the hypothesis of Andean vicariance as the origen of diversification for *Liolaemus*. Models of central Andean uplift predict an altitude at that time of no more than 1000-1500 m a.s.l. (Gregory-Wodzicki 2002, Garzione et al. 2008, Barnes and Ehlers 2009, Leier et al. 2013, Fiorella et al. 2015), considering that global temperatures were around 5 degrees warmer than today during that period (Zachos et al. 2008) (Figure 4C) those altitudes probably did not constitute a major barrier for dispersal. This does not favor the hypothesis of Andean vicariance to explain the *Liolaemus-Eulaemus* split (Schulte et al. 2000). Furthermore, during late Oligocene-Early Miocene (26-20 mya) an Atlantic introgression flooded much of southern Argentina creating a “Patagonian Sea” and isolating east and west areas in the Argentinian Patagonia (Ortiz-Jaureguizar and Cladera 2006), which is consistent with the timing of *Liolaemus-Eulaemus* split. Global temperatures show a continuous drop from mid Oligocene (≈ 45 mya) until approximately 30 mya when it remained stable for around 15 mya (Zachos et al. 2001), (Figure 4C). Nevertheless, crustal shortening was becoming more intense at that time (Figure 4B) which would have caused important landscape changes (more cliffy and rugged) which may have provided ecological opportunity for the diversification of *Liolaemus*.

Regarding presence in Argentina of *Liolaemus* s.s. clades, we find the age of the split between *L. petrophylus* and *leopardinus* group to be 11 mya and the age of the split between *L. bibroni* and *L. paulinae* 13 mya (Figure 2A). Up until that time, the central Andes were, on average, less than half its current height (Figure 4B); considering that global temperatures were 4 to 5 degrees higher than now the cordillera was probably not a strong barrier for *Liolaemus* dispersal. Those dates are consistent with two climatic events: On one hand, the onset of aridification by rain shadow (Gregory-Wodzicki 2000) and on the other hand, the timing when global temperatures started to drop (Figure 4B-C). Therefore, although vicariance by Andean uplift was probably not responsible of the *Liolaemus-Eulaemus* split, it probably was for the separation of the Argentinian members of *Liolaemus* s.s. (the *bibroni* group and the *petrophylus* group).

The spectral density analysis as well as the MCCR test are inconsistent with an early burst. Further the positive gamma statistic suggests a late diversification; this differs from Pincheira-Donoso et al. (2015) who found a negative γ, although the test was not significant. This also means that if ecological opportunity is the main driver of the radiation of Liolaemus, the opening of new niches was gradual. This is consistent with the findings from Pincheira-Donoso et al. (2015) and with gradual geological processes such as orogeny or gradual changes in climate rather than rapid colonization of new geographical areas such as island colonization (Pincheira-Donoso et al. 2015 and references within). A gradual and constant diversification rate since the *Liolaemus-Eulaemus* split is also supported by the the LTT plot (Figure 4A).

The two subgenera, nevertheless, did not share the same pattern of diversification. The *Eulaemus* clade appears to have started its own diversification later than *Liolaemus* s.s. (Figure 4A). Our phylogeny recovers the main split within *Eulaemus* at 19 mya and the main split within *Liolaemus* s.s. at 241 mya. In addition, *Liolaemus* s.s. shows signs of an earlier type of diversification while *Eulaemus* seems to diversify faster towards more recent times (Figure 3, Table 1). These contrasting patterns in each of the main subclades explain why the general pattern in the LTT plot shows a linear diversification. Both subgenera are, to a large extent, separated geographically, being *Eulaemus* absent from the west slope of the Andes north of the Patagonia region which is occupied by the vast majority of *Liolaemus* s.s. species. *Anolis* shows differences in diversification in Caribean islands and on the mainland (Velasco et al. 2016) as those are associated with different climates and niche traits. Therefore it is reasonable to expect that even if the clade as a whole has experienced a constant diversification, subclades may show relatively independent patterns of diversification (Alfaro et al. 2009). Changes in diversification patterns have been related with trophic and functional shifts (Wiegmann et al. 2011) although in the case of *Liolaemus* both subgenera include species from a wide variety of habitats and life history traits.

In agreement with the results of Pincheira-Donoso (2015), *Liolaemus* diversification rate appears constant since the start of their diversification (Fig 3A), that makes difficult that any of the variables may improve the time-dependent model. Nevertheless, as mentioned above, the two main clades within the genus do not follow the same pattern, with *Liolaemus* s.s. showing an early pattern of diversification and *Eulaemus* a slightly accelerating pattern (Figure 3D). Although, none of the variables improves *Liolaemus* ss. models, in *Eulaemus*, on the other hand, we find that the models fitted with temperature change (for crown age) have lower AICc (Table 2), suggesting an effect of climate in *Eulaemus* diversification. *Liolaemus* is one of the few reptile groups in South America characteristic of cold and temperate climates. The oldest fossil attributed to *Liolaemus* comes from Southern Argentinian Patagonia (in the Chubut region) (Albino 2008). The progressive cooling of the climate since mid-Miocene may have allowed *Liolaemus* to expand its range to the north as tropical climates become more temperate and the number of niches available increased as more tropical taxa (such as teiids or boids) disappeared from their landscape (Albino 2011).

According to our results *Liolaemus* clade may be older than previously suggested, their origin being not too far from the extinction of non avian dinosaurs. The first split within the group also seems older than previously proposed, questioning even more the Andean vicariance as the origin of diversification of the group which, on the other hand, may explain the presence of some *Liolaemus* s.s. species east of the Andes. This geographical separation of the clades also reflects in the different pattern of diversifications between the two main groups.

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SUPPORTING INFORMATION

Figure S1
Figure S2
Table S1
Table S2
Table S3

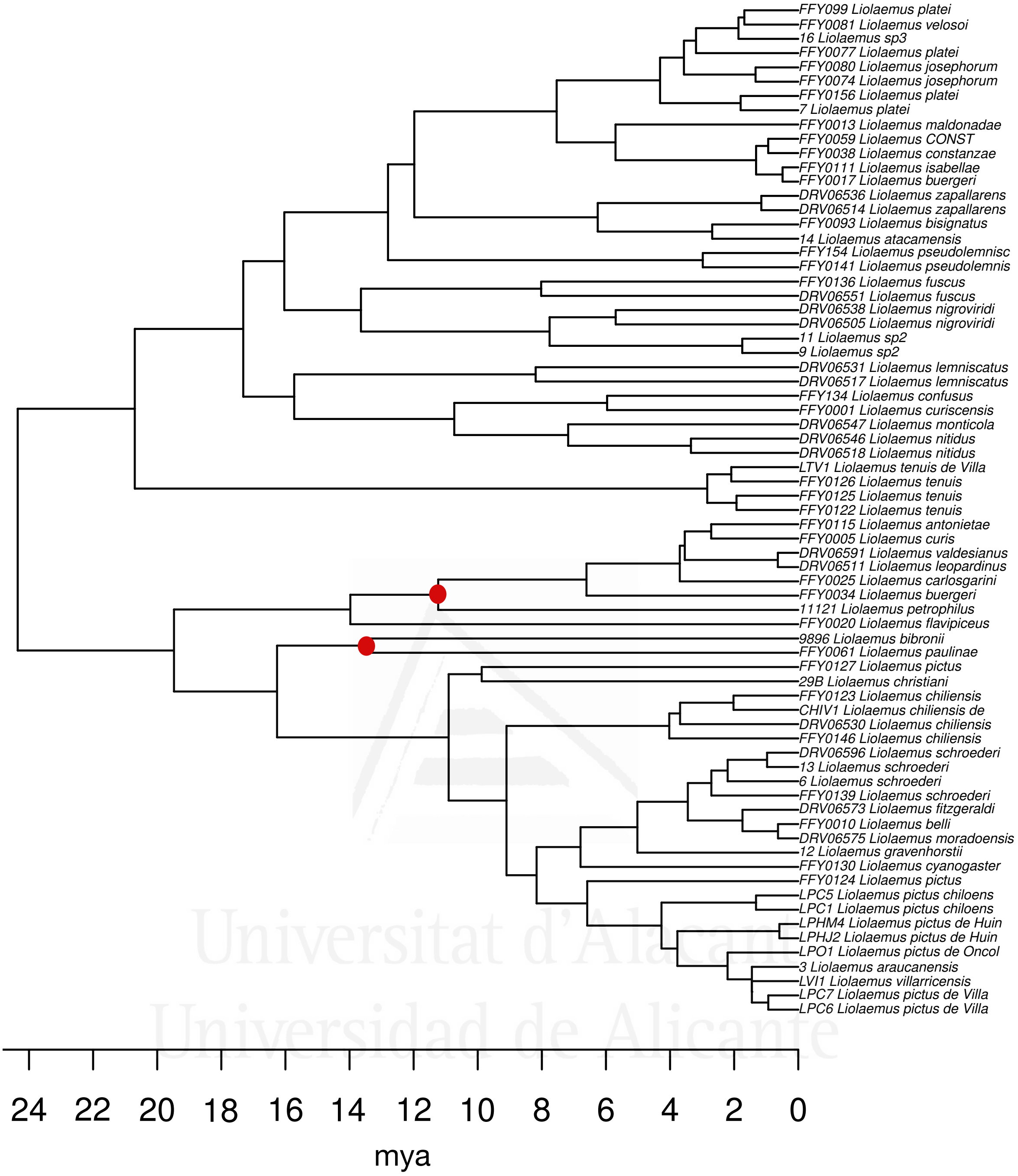


Figure S1. Complete time calibrated phylogeny of subgenus *Liolaemus* sensu stricto. Red dots mark the nodes between species of both sides of the Andes.

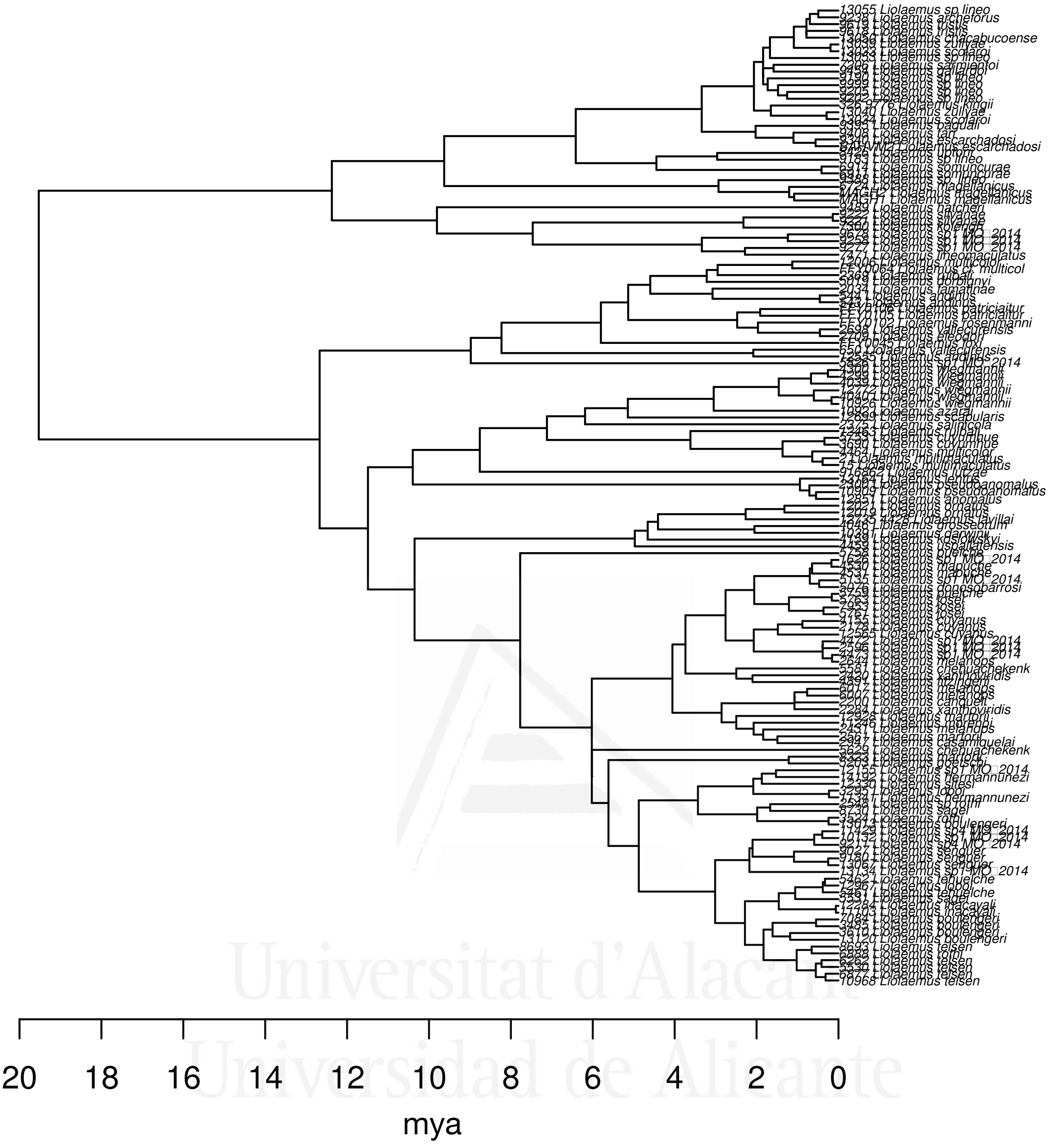


Figure S2. Complete time calibrated phylogeny of subgenus *Eulaemus*.

Table S1. Primers used in this study. 1 Troncoso-Palacios et al. 2015 Zootaxa.

Locus	Primer name	Primer sequence	Melting temperature	Reference
12S	LIO_DRV_12S_F	5'-CATCCGCAYMCCAGTGAGAATGCC-3'	62.1	1
	LIO_DRV_12S_R	5'-GAGGAGGGTGACGGGCGGTGTGTG-3'	67.5	1
CYTB	LIO_DRV_CYTB_F	5'-CCCATCAAACATCTCTGCMTGATG-3'	57.1	1
	LIO_DRV_CYTB_R	5'-TGGTGTRAAGTTTTCTGGGTCTCC-3'	57.9	1
C-MOS	LIO_DRV_CMOS_F	5'-AGTAAGAATAGTTTGGCATCACGG-3'	55.1	This study
	LIO_DRV_CMOS_R	5'-TCAGGGGCACGATGAGTGTATGTC-3'	60.5	This study
MXRA5	LIO_DRV_MXRA5_F	5'-AGTAGTGCTCTCTTTTTCTACCAG-3'	54.1	This study
	LIO_DRV_MXRA5_R	5'-ATCTGAGCAGCAGAAACATGG-3'	55.4	This study
KIF24	LIO_DRV_KIF24_F	5'-CAGAGCTCCCCTTGCGYACAAACG-3'	63.3	This study
	LIO_DRV_KIF24_R	5'-TGGAATTGCTGGTGGTAAAGGCGG-3'	61.9	This study
PNN	LIO_DRV_PNN_F	5'-GTAGAAATGGAAGAGGCAGGGGAG-3'	59	This study
	LIO_DRV_PNN_R	5'-TCTGATATAGACCTCTTTCTGTCCGAC-3'	57	This study
PRLR	LIO_DRV_PRLR_F	5'-ACCAGCAACTGATGCCGAATCATG-3'	60	This study
	LIO_DRV_PRLR_R	5'-CTTCCACGTAATCCATTGGCTTTG-3'	56.6	This study

Table S2. Genbank accession numbers for Argentinian *Liolaemus*.

Gene	Sample	Genbank	bp	Sp	Gene	Sample	Genbank	bp	Sp
12S	2	KF969088	786	*L.multimaculatus*	KIF24	5629	KF968083	467	*L.chehuachekenk*
12S	326	KF969053	789	*L.kingii*	KIF24	5753	KF968087	465	*L.cuyumhue*
12S	543	KF968999	789	*L.andinus*	KIF24	5758	KF968155	467	*L.puelche*
12S	544	KF969000	788	*L.andinus*	KIF24	5761	KF968111	467	*L.josei*
12S	650	KF969166	784	*L.vallecurensis*	KIF24	5763	KF968112	467	*L.josei*
12S	1092	KF969005	782	*L.azarai*	KIF24	5826	KF968184	467	*L.sp.1*
12S	1626	KF969124	759	*L.sp.1*	KIF24	6007	KF968139	467	*L.melanops*
12S	2034	KF969038	787	*L.famatinae*	KIF24	6017	KF968140	467	*L.melanops*
12S	2178	KF969025	787	*L.cuyanus*	KIF24	6262	KF968253	534	*L.telsen*
12S	2200	KF969016	787	*L.canqueli*	KIF24	6724	KF968129	467	*L.magellanicus*
12S	2300	KF969095	747	*L.pseudoanomalus*	KIF24	6877	KF968254	534	*L.telsen*
12S	2369	KF969101	782	*L.ruibali*	KIF24	6888	KF968158	467	*L.rothi*
12S	2375	KF969107	772	*L.salinicola*	KIF24	6911	KF968173	467	*L.somuncurae*
12S	2420	KF969177	787	*L.xanthoviridis*	KIF24	6914	KF968174	467	*L.somuncurae*
12S	2431	KF969076	785	*L.melanops*	KIF24	7084	KF968077	467	*L.boulengeri*
12S	2548	KF969148	785	*L.sp.*	KIF24	7206	KF968166	467	*L.sarmientoi*
12S	2561	KF969073	778	*L.martorii*	KIF24	7300	KF968115	467	*L.kolengh*
12S	2596	KF969150	787	*L.sp.1*	KIF24	7471	KF968121	467	*L.lineomaculatus*
12S	2644	KF969082	787	*L.melanops*	KIF24	7953	KF968113	467	*L.josei*
12S	2698	KF969165	783	*L.vallecurensis*	KIF24	8323	KF968134	467	*L.martorii*
12S	2709	KF969034	734	*L.eleodori*	KIF24	8426	KF968216	467	*L.uptoni*
12S	2947	KF969018	764	*L.casamiquelai*	KIF24	8693	KF968213	467	*L.telsen*
12S	3295	KF969065	780	*L.loboi*	KIF24	8730	KF968161	467	*L.sagei*
12S	3485	KF969197	869	*L.boulengeri*	KIF24	9027	KF968257	534	*L.senguer*
12S	3524	KF969198	867	*L.rothi*	KIF24	9183	KF968190	467	*L.sp.lineo*
12S	3610	KF969012	786	*L.boulengeri*	KIF24	9190	KF968191	467	*L.sp.lineo*
12S	3690	KF969028	787	*L.cuyumhue*	KIF24	9202	KF968192	467	*L.sp.lineo*
12S	4039	KF969172	783	*L.wiegmannii*	KIF24	9205	KF968193	467	*L.sp.lineo*
12S	4040	KF969173	781	*L.wiegmannii*	KIF24	9222	KF968172	467	*L.silvanae*
12S	4046	KF969042	786	*L.grosseorum*	KIF24	9238	KF968068	467	*L.archeforus*
12S	4155	KF969024	779	*L.cuyanus*	KIF24	9258	KF968175	467	*L.sp.1*
12S	4159	KF969056	785	*L.koslowskyi*	KIF24	9277	KF968177	467	*L.sp.1*
12S	4299	KF969167	783	*L.wiegmannii*	KIF24	9340	KF968096	467	*L.escarchadosi*
12S	4300	KF969168	783	*L.wiegmannii*	KIF24	9388	KF968194	467	*L.sp.lineo*
12S	4459	KF969164	783	*L.uspallatensis*	KIF24	9395	KF968072	467	*L.baguali*
12S	4464	KF969087	786	*L.multicolor*	KIF24	9408	KF968209	467	*L.tari*
12S	4472	KF969152	788	*L.sp.1*	KIF24	9454	KF968100	467	*L.gallardoi*
12S	4473	KF969153	697	*L.sp.1*	KIF24	9489	KF968103	467	*L.hatcheri*
12S	4530	KF969070	788	*L.mapuche*	KIF24	9618	KF968214	467	*L.tristis*
12S	4531	KF969071	787	*L.mapuche*	KIF24	9619	KF968215	467	*L.tristis*
12S	4665	KF969017	787	*L.canqueli*	KIF24	9678	KF968178	467	*L.sp.1*
12S	4891	KF969039	741	*L.fitzingerii*	KIF24	9896	KF968073	470	*L.bibronii*
12S	5019	KF969033	787	*L.dorbignyi*	KIF24	9999	KF968196	467	*L.sp.lineo*
12S	5076	KF969031	785	*L.donosobarrosi*	KIF24	10132	KF968182	467	*L.sp.1*
12S	5135	KF969143	759	*L.sp.1*	KIF24	10391	KF968089	465	*L.darwinii*
12S	5203	KF969041	785	*L.goetschi*	KIF24	10909	KF968153	465	*L.pseudoanomalus*
12S	5461	KF969156	784	*L.tehuelche*	KIF24	10926	KF968225	465	*L.wiegmannii*
12S	5462	KF969157	784	*L.tehuelche*	KIF24	10968	KF968236	534	*L.telsen*

Gene	Sample	Genbank	bp	Sp	Gene	Sample	Genbank	bp	Sp
12S	5531	KF969103	786	*L.sagei*	KIF24	11103	KF968108	467	*L.inacayali*
12S	5581	KF969023	786	*L.chehuachekenk*	KIF24	11246	KF968142	467	*L.morenoi*
12S	5628	KF969021	705	*L.chehuachekenk*	KIF24	11341	KF968107	467	*L.hermannunezi*
12S	5629	KF969022	787	*L.chehuachekenk*	KIF24	11429	KF968238	534	*L.sp.4*
12S	5753	KF969027	786	*L.cuyumhue*	KIF24	12006	KF968144	465	*L.multicolor*
12S	5759	KF969096	787	*L.puelche*	KIF24	12019	KF968148	465	*L.ornatus*
12S	5761	KF969050	786	*L.josei*	KIF24	12021	KF968149	457	*L.ornatus*
12S	5763	KF969051	787	*L.josei*	KIF24	12155	KF968180	467	*L.sp.1*
12S	5826	KF969130	787	*L.sp.1*	KIF24	12284	KF968239	534	*L.inacayali*
12S	6007	KF969080	787	*L.melanops*	KIF24	12330	KF968242	534	*L.sitesi*
12S	6017	KF969081	788	*L.melanops*	KIF24	12463	KF968159	465	*L.ruibali*
12S	6262	KF969199	828	*L.telsen*	KIF24	12555	KF968066	465	*L.andinus*
12S	6724	KF969069	790	*L.magellanicus*	KIF24	12565	KF968086	467	*L.cuyanus*
12S	6877	KF969200	864	*L.telsen*	KIF24	12699	KF968168	465	*L.scapularis*
12S	6888	KF969100	743	*L.rothi*	KIF24	12772	KF968230	467	*L.wiegmannii*
12S	6911	KF969118	787	*L.somuncurae*	KIF24	12851	KF968067	465	*L.anomalus*
12S	6914	KF969119	787	*L.somuncurae*	KIF24	12928	KF968132	467	*L.martorii*
12S	7084	KF969014	787	*L.boulengeri*	KIF24	12967	KF968124	467	*L.loboi*
12S	7206	KF969109	790	*L.sarmientoi*	KIF24	13013	KF968075	467	*L.boulengeri*
12S	7300	KF969055	788	*L.kolengh*	KIF24	13033	KF968169	460	*L.scolaroi*
12S	7471	KF969061	789	*L.lineomaculatus*	KIF24	13034	KF968170	434	*L.scolaroi*
12S	7953	KF969052	786	*L.josei*	KIF24	13039	KF968234	467	*L.zullyae*
12S	8323	KF969074	739	*L.martorii*	KIF24	13040	KF968235	460	*L.zullyae*
12S	8426	KF969161	789	*L.uptoni*	KIF24	13050	KF968081	460	*L.chacabucoense*
12S	8693	KF969158	784	*L.telsen*	KIF24	13053	KF968187	460	*L.sp.lineo*
12S	8730	KF969104	785	*L.sagei*	KIF24	13055	KF968188	461	*L.sp.lineo*
12S	9027	KF969203	829	*L.senguer*	KIF24	13134	KF968185	467	*L.sp.1*
12S	9183	KF969136	789	*L.sp.lineo*	KIF24	13164	KF968120	436	*L.lentus*
12S	9190	KF969137	789	*L.sp.lineo*	KIF24	14192	KF968105	467	*L.hermannunezi*
12S	9202	KF969138	788	*L.sp.lineo*	KIF24	916862	KF968127	465	*L.lutzae*
12S	9205	KF969139	789	*L.sp.lineo*	KIF24	13067	KF968244	535	*L.Liolaemus*
12S	9211	KF969205	860	*L.sp.4*	KIF24	13120	KF968245	525	*L.boulengeri*
12S	9221	KF969116	789	*L.silvanae*	MXRA5	2	KF967999	827	*L.multimaculatus*
12S	9222	KF969117	789	*L.silvanae*	MXRA5	326	KF967976	827	*L.kingii*
12S	9238	KF969003	789	*L.archeforus*	MXRA5	544	KF967948	827	*L.andinus*
12S	9258	KF969120	789	*L.sp.1*	MXRA5	2034	KF967965	827	*L.famatinae*
12S	9277	KF969122	789	*L.sp.1*	MXRA5	2200	KF967954	827	*L.canqueli*
12S	9340	KF969036	789	*L.escarchadosi*	MXRA5	2284	KF968045	827	*L.xanthoviridis*
12S	9388	KF969140	789	*L.sp.lineo*	MXRA5	2300	KF968006	827	*L.pseudoanomalus*
12S	9395	KF969008	789	*L.baguali*	MXRA5	2369	KF968011	827	*L.ruibali*
12S	9408	KF969155	789	*L.tari*	MXRA5	2431	KF967991	824	*L.melanops*
12S	9454	KF969040	789	*L.gallardoi*	MXRA5	2548	KF968031	827	*L.sp.*
12S	9489	KF969043	789	*L.hatcheri*	MXRA5	2596	KF968033	827	*L.sp.1*
12S	9618	KF969159	789	*L.tristis*	MXRA5	2644	KF967995	827	*L.melanops*
12S	9619	KF969160	789	*L.tristis*	MXRA5	3295	KF967983	827	*L.loboi*
12S	9678	KF969123	789	*L.sp.1*	MXRA5	3485	KF968057	864	*L.boulengeri*
12S	9896	KF969009	785	*L.bibronii*	MXRA5	3524	KF968058	864	*L.rothi*
12S	9999	KF969142	789	*L.sp.*	MXRA5	3610	KF967951	827	*L.boulengeri*
12S	10132	KF969128	784	*L.sp.1*	MXRA5	4039	KF968042	827	*L.wiegmannii*
12S	10391	KF969029	785	*L.darwinii*	MXRA5	4046	KF967967	827	*L.grosseorum*
12S	10909	KF969094	784	*L.pseudoanomalus*	MXRA5	4159	KF967978	827	*L.koslowskyi*

Gene	Sample	Genbank	bp	Sp	Gene	Sample	Genbank	bp	Sp
12S	10926	KF969170	779	*L.wiegmannii*	MXRA5	4473	KF968034	827	*L.sp.1*
12S	10968	KF969182	866	*L.telsen*	MXRA5	4531	KF967988	827	*L.mapuche*
12S	11103	KF969048	787	*L.inacayali*	MXRA5	5019	KF967963	827	*L.dorbignyi*
12S	11246	KF969083	784	*L.morenoi*	MXRA5	5076	KF967962	827	*L.donosobarrosi*
12S	11341	KF969047	788	*L.hermannunezi*	MXRA5	5135	KF968028	827	*L.sp.1*
12S	11429	KF969184	832	*L.sp.4*	MXRA5	5203	KF967966	827	*L.goetschi*
12S	12006	KF969085	787	*L.multicolor*	MXRA5	5462	KF968035	827	*L.tehuelche*
12S	12019	KF969089	783	*L.ornatus*	MXRA5	5530	KF968036	827	*L.telsen*
12S	12021	KF969090	783	*L.ornatus*	MXRA5	5531	KF968012	827	*L.sagei*
12S	12155	KF969126	786	*L.sp.1*	MXRA5	5581	KF967957	827	*L.chehuachekenk*
12S	12284	KF969185	838	*L.inacayali*	MXRA5	5629	KF967956	827	*L.chehuachekenk*
12S	12330	KF969188	858	*L.sitesi*	MXRA5	5753	KF967959	827	*L.cuyumhue*
12S	12463	KF969102	786	*L.ruibali*	MXRA5	5761	KF967973	827	*L.josei*
12S	12555	KF969001	784	*L.andinus*	MXRA5	5763	KF967974	827	*L.josei*
12S	12565	KF969026	781	*L.cuyanus*	MXRA5	5826	KF968026	827	*L.sp.1*
12S	12699	KF969111	786	*L.scapularis*	MXRA5	6007	KF967993	827	*L.melanops*
12S	12772	KF969175	780	*L.wiegmannii*	MXRA5	6017	KF967994	827	*L.melanops*
12S	12851	KF969002	782	*L.anomalus*	MXRA5	6262	KF968059	865	*L.telsen*
12S	12894	KF969146	785	*L.sp.1*	MXRA5	6724	KF967987	827	*L.magellanicus*
12S	12928	KF969072	785	*L.martorii*	MXRA5	6877	KF968060	864	*L.telsen*
12S	12967	KF969064	784	*L.loboi*	MXRA5	6888	KF968010	827	*L.rothi*
12S	13013	KF969011	785	*L.boulengeri*	MXRA5	6911	KF968017	548	*L.somuncurae*
12S	13033	KF969112	789	*L.scolaroi*	MXRA5	7084	KF967952	827	*L.boulengeri*
12S	13034	KF969113	789	*L.scolaroi*	MXRA5	7300	KF967977	544	*L.kolengh*
12S	13039	KF969178	789	*L.zullyae*	MXRA5	7471	KF967980	538	*L.lineomaculatus*
12S	13040	KF969179	789	*L.zullyae*	MXRA5	7953	KF967975	532	*L.josei*
12S	13050	KF969020	789	*L.chacabucoense*	MXRA5	8323	KF967990	827	*L.martorii*
12S	13053	KF969133	789	*L.sp.lineo*	MXRA5	8693	KF968037	827	*L.telsen*
12S	13055	KF969134	789	*L.sp.lineo*	MXRA5	8730	KF968013	801	*L.sagei*
12S	13067	KF969190	866	*L.senguer*	MXRA5	9027	KF968063	864	*L.senguer*
12S	13120	KF969192	869	*L.boulengeri*	MXRA5	9221	KF968016	810	*L.silvanae*
12S	13134	KF969131	785	*L.sp.1*	MXRA5	9258	KF968018	548	*L.sp.1*
12S	13164	KF969060	783	*L.lentus*	MXRA5	9277	KF968020	515	*L.sp.1*
12S	14192	KF969045	786	*L.hermannunezi*	MXRA5	9395	KF967949	827	*L.baguali*
12S	916862	KF969067	786	*L.lutzae*	MXRA5	9489	KF967968	548	*L.hatcheri*
CMOS	9211	KF968821	527	*L.sp.4*	MXRA5	9678	KF968021	547	*L.sp.1*
CMOS	2	KF968711	481	*L.multimaculatus*	MXRA5	10132	KF968024	827	*L.sp.1*
CMOS	15	KF968710	481	*L.multimaculatus*	MXRA5	10909	KF968005	817	*L.pseudoanomalus*
CMOS	326	KF968680	472	*L.kingii*	MXRA5	10926	KF968041	827	*L.wiegmannii*
CMOS	543	KF968628	481	*L.andinus*	MXRA5	11246	KF967996	827	*L.morenoi*
CMOS	544	KF968629	481	*L.andinus*	MXRA5	11341	KF967970	827	*L.hermannunezi*
CMOS	650	KF968785	481	*L.vallecurensis*	MXRA5	11429	KF968048	864	*L.sp.4*
CMOS	1092	KF968634	481	*L.azarai*	MXRA5	12019	KF968000	827	*L.ornatus*
CMOS	1626	KF968744	481	*L.sp.1*	MXRA5	12021	KF968001	827	*L.ornatus*
CMOS	2034	KF968666	481	*L.famatinae*	MXRA5	12155	KF968022	827	*L.sp.1*
CMOS	2178	KF968653	481	*L.cuyanus*	MXRA5	12284	KF968049	862	*L.inacayali*
CMOS	2200	KF968644	481	*L.canqueli*	MXRA5	12330	KF968050	783	*L.sitesi*
CMOS	2284	KF968795	481	*L.xanthoviridis*	MXRA5	12565	KF967958	827	*L.cuyanus*
CMOS	2300	KF968717	481	*L.pseudoanomalus*	MXRA5	12772	KF968044	827	*L.wiegmannii*
CMOS	2369	KF968723	481	*L.ruibali*	MXRA5	12928	KF967989	827	*L.martorii*
CMOS	2375	KF968729	481	*L.salinicola*	MXRA5	12967	KF967982	827	*L.loboi*

Gene	Sample	Genbank	bp	Sp	Gene	Sample	Genbank	bp	Sp
CMOS	2420	KF968796	481	*L.xanthoviridis*	MXRA5	13013	KF967950	827	*L.boulengeri*
CMOS	2431	KF968699	481	*L.melanops*	MXRA5	13067	KF968052	864	*L.senguer*
CMOS	2548	KF968767	446	*L.sp.*	MXRA5	13120	KF968054	859	*L.boulengeri*
CMOS	2596	KF968769	481	*L.sp.1*	MXRA5	916862	KF967985	827	*L.lutzae*
CMOS	2644	KF968704	481	*L.melanops*	MXRA5	2698	KF968040	826	*L.Liolaemus*
CMOS	2698	KF968784	481	*L.vallecurensis*	MXRA5	2709	KF967964	826	*L.Liolaemus*
CMOS	2709	KF968662	475	*L.eleodori*	MXRA5	4459	KF968039	826	*L.Liolaemus*
CMOS	2947	KF968646	481	*L.casamiquelai*	MXRA5	4464	KF967998	826	*L.Liolaemus*
CMOS	3295	KF968691	481	*L.loboi*	MXRA5	10391	KF967960	662	*L.Liolaemus*
CMOS	3485	KF968814	528	*L.boulengeri*	MXRA5	10968	KF968046	864	*L.Liolaemus*
CMOS	3524	KF968815	528	*L.rothi*	MXRA5	11103	KF967971	826	*L.Liolaemus*
CMOS	3610	KF968640	481	*L.boulengeri*	PNN	9211	KF967947	695	*L.sp.4*
CMOS	3690	KF968656	481	*L.cuyumhue*	PNN	2	KF967835	887	*L.multimaculatus*
CMOS	4039	KF968790	481	*L.wiegmannii*	PNN	15	KF967834	887	*L.multimaculatus*
CMOS	4040	KF968791	481	*L.wiegmannii*	PNN	326	KF967803	887	*L.kingii*
CMOS	4046	KF968670	481	*L.grosseorum*	PNN	543	KF967755	887	*L.andinus*
CMOS	4155	KF968652	481	*L.cuyanus*	PNN	544	KF967756	887	*L.andinus*
CMOS	4159	KF968683	481	*L.koslowskyi*	PNN	650	KF967911	887	*L.vallecurensis*
CMOS	4299	KF968786	481	*L.wiegmannii*	PNN	1092	KF967761	887	*L.azarai*
CMOS	4459	KF968783	446	*L.uspallatensis*	PNN	1626	KF967869	887	*L.sp.1*
CMOS	4464	KF968709	481	*L.multicolor*	PNN	2034	KF967788	887	*L.famatinae*
CMOS	4472	KF968771	481	*L.sp.1*	PNN	2178	KF967777	887	*L.cuyanus*
CMOS	4473	KF968772	481	*L.sp.1*	PNN	2200	KF967770	887	*L.canqueli*
CMOS	4530	KF968695	481	*L.mapuche*	PNN	2284	KF967922	887	*L.xanthoviridis*
CMOS	4891	KF968667	481	*L.fitzingerii*	PNN	2300	KF967841	829	*L.pseudoanomalus*
CMOS	5019	KF968661	481	*L.dorbignyi*	PNN	2375	KF967853	887	*L.salinicola*
CMOS	5076	KF968659	481	*L.donosobarrosi*	PNN	2420	KF967923	887	*L.xanthoviridis*
CMOS	5135	KF968762	481	*L.sp.1*	PNN	2431	KF967824	887	*L.melanops*
CMOS	5203	KF968669	481	*L.goetschi*	PNN	2548	KF967893	887	*L.sp.*
CMOS	5461	KF968775	481	*L.tehuelche*	PNN	2561	KF967821	887	*L.martorii*
CMOS	5462	KF968776	481	*L.tehuelche*	PNN	2596	KF967895	887	*L.sp.1*
CMOS	5530	KF968777	481	*L.telsen*	PNN	2698	KF967910	887	*L.vallecurensis*
CMOS	5531	KF968725	481	*L.sagei*	PNN	3295	KF967813	887	*L.loboi*
CMOS	5581	KF968651	481	*L.chehuachekenk*	PNN	3485	KF967939	950	*L.boulengeri*
CMOS	5629	KF968650	481	*L.chehuachekenk*	PNN	3524	KF967940	921	*L.rothi*
CMOS	5753	KF968655	481	*L.cuyumhue*	PNN	3610	KF967767	887	*L.boulengeri*
CMOS	5758	KF968718	481	*L.puelche*	PNN	3690	KF967780	887	*L.cuyumhue*
CMOS	5759	KF968719	481	*L.puelche*	PNN	4039	KF967917	887	*L.wiegmannii*
CMOS	5761	KF968677	481	*L.josei*	PNN	4040	KF967918	887	*L.wiegmannii*
CMOS	5763	KF968678	481	*L.josei*	PNN	4155	KF967776	887	*L.cuyanus*
CMOS	5826	KF968750	481	*L.sp.1*	PNN	4159	KF967805	887	*L.koslowskyi*
CMOS	6007	KF968702	481	*L.melanops*	PNN	4299	KF967912	887	*L.wiegmannii*
CMOS	6017	KF968703	481	*L.melanops*	PNN	4300	KF967913	887	*L.wiegmannii*
CMOS	6262	KF968816	528	*L.telsen*	PNN	4459	KF967909	887	*L.uspallatensis*
CMOS	6724	KF968694	481	*L.magellanicus*	PNN	4472	KF967896	887	*L.sp.1*
CMOS	6877	KF968817	528	*L.telsen*	PNN	4473	KF967897	887	*L.sp.1*
CMOS	6888	KF968722	481	*L.rothi*	PNN	4530	KF967818	887	*L.mapuche*
CMOS	6914	KF968740	480	*L.somuncurae*	PNN	4531	KF967819	887	*L.mapuche*
CMOS	7084	KF968642	481	*L.boulengeri*	PNN	4891	KF967789	887	*L.fitzingerii*
CMOS	7206	KF968731	480	*L.sarmientoi*	PNN	5019	KF967785	887	*L.dorbignyi*
CMOS	7300	KF968682	480	*L.kolengh*	PNN	5076	KF967783	887	*L.donosobarrosi*

Gene	Sample	Genbank	bp	Sp	Gene	Sample	Genbank	bp	Sp
CMOS	7471	KF968687	481	*L.lineomaculatus*	PNN	5135	KF967888	887	*L.sp.1*
CMOS	7953	KF968679	481	*L.josei*	PNN	5203	KF967791	887	*L.goetschi*
CMOS	8323	KF968697	448	*L.martorii*	PNN	5461	KF967900	887	*L.tehuelche*
CMOS	8426	KF968780	480	*L.uptoni*	PNN	5462	KF967901	887	*L.tehuelche*
CMOS	8693	KF968778	481	*L.telsen*	PNN	5530	KF967902	887	*L.telsen*
CMOS	8730	KF968726	481	*L.sagei*	PNN	5531	KF967849	887	*L.sagei*
CMOS	9027	KF968819	527	*L.senguer*	PNN	5581	KF967775	887	*L.chehuachekenk*
CMOS	9183	KF968756	480	*L.sp.lineo*	PNN	5629	KF967774	887	*L.chehuachekenk*
CMOS	9190	KF968757	452	*L.sp.lineo*	PNN	5753	KF967779	856	*L.cuyumhue*
CMOS	9202	KF968758	435	*L.sp.lineo*	PNN	5758	KF967842	887	*L.puelche*
CMOS	9205	KF968759	478	*L.sp.lineo*	PNN	5759	KF967843	887	*L.puelche*
CMOS	9221	KF968738	480	*L.silvanae*	PNN	5761	KF967800	887	*L.josei*
CMOS	9222	KF968739	481	*L.silvanae*	PNN	5763	KF967801	887	*L.josei*
CMOS	9238	KF968632	481	*L.archeforus*	PNN	5826	KF967875	887	*L.sp.1*
CMOS	9258	KF968741	481	*L.sp.1*	PNN	6007	KF967827	887	*L.melanops*
CMOS	9277	KF968742	480	*L.sp.1*	PNN	6017	KF967828	887	*L.melanops*
CMOS	9340	KF968664	477	*L.escarchadosi*	PNN	6262	KF967941	938	*L.telsen*
CMOS	9388	KF968760	480	*L.sp.lineo*	PNN	6724	KF967817	887	*L.magellanicus*
CMOS	9395	KF968636	480	*L.baguali*	PNN	6877	KF967942	909	*L.telsen*
CMOS	9408	KF968774	481	*L.tari*	PNN	6888	KF967847	887	*L.rothi*
CMOS	9454	KF968668	481	*L.gallardoi*	PNN	6911	KF967864	887	*L.somuncurae*
CMOS	9489	KF968671	480	*L.hatcheri*	PNN	6914	KF967865	869	*L.somuncurae*
CMOS	9619	KF968779	481	*L.tristis*	PNN	7084	KF967768	887	*L.boulengeri*
CMOS	9678	KF968743	480	*L.sp.1*	PNN	7206	KF967855	887	*L.sarmientoi*
CMOS	9896	KF968637	481	*L.bibronii*	PNN	7300	KF967804	887	*L.kolengh*
CMOS	9999	KF968761	461	*L.sp.lineo*	PNN	7471	KF967809	887	*L.lineomaculatus*
CMOS	10132	KF968748	481	*L.sp.1*	PNN	7953	KF967802	887	*L.josei*
CMOS	10391	KF968657	481	*L.darwinii*	PNN	8323	KF967822	887	*L.martorii*
CMOS	10909	KF968716	481	*L.pseudoanomalus*	PNN	8426	KF967906	887	*L.uptoni*
CMOS	10926	KF968788	481	*L.wiegmannii*	PNN	8693	KF967903	887	*L.telsen*
CMOS	10968	KF968801	528	*L.telsen*	PNN	8730	KF967850	887	*L.sagei*
CMOS	11103	KF968675	481	*L.inacayali*	PNN	9027	KF967945	927	*L.senguer*
CMOS	11246	KF968705	481	*L.morenoi*	PNN	9183	KF967881	887	*L.sp.lineo*
CMOS	11341	KF968674	481	*L.hermannunezi*	PNN	9190	KF967882	887	*L.sp.lineo*
CMOS	11429	KF968803	528	*L.sp.4*	PNN	9202	KF967883	887	*L.sp.lineo*
CMOS	12006	KF968707	481	*L.multicolor*	PNN	9205	KF967884	887	*L.sp.lineo*
CMOS	12019	KF968712	481	*L.ornatus*	PNN	9221	KF967862	887	*L.silvanae*
CMOS	12021	KF968713	481	*L.ornatus*	PNN	9222	KF967863	887	*L.silvanae*
CMOS	12155	KF968746	481	*L.sp.1*	PNN	9238	KF967759	887	*L.archeforus*
CMOS	12284	KF968804	494	*L.inacayali*	PNN	9258	KF967866	887	*L.sp.1*
CMOS	12330	KF968806	528	*L.sitesi*	PNN	9277	KF967867	887	*L.sp.1*
CMOS	12463	KF968724	481	*L.ruibali*	PNN	9340	KF967786	887	*L.escarchadosi*
CMOS	12555	KF968630	481	*L.andinus*	PNN	9388	KF967885	887	*L.sp.lineo*
CMOS	12565	KF968654	481	*L.cuyanus*	PNN	9395	KF967763	887	*L.baguali*
CMOS	12699	KF968733	481	*L.scapularis*	PNN	9408	KF967899	885	*L.tari*
CMOS	12772	KF968793	481	*L.wiegmannii*	PNN	9454	KF967790	887	*L.gallardoi*
CMOS	12851	KF968631	481	*L.anomalus*	PNN	9489	KF967792	887	*L.hatcheri*
CMOS	12928	KF968696	481	*L.martorii*	PNN	9618	KF967904	887	*L.tristis*
CMOS	12967	KF968690	481	*L.loboi*	PNN	9619	KF967905	887	*L.tristis*
CMOS	13013	KF968639	481	*L.boulengeri*	PNN	9678	KF967868	887	*L.sp.1*
CMOS	13033	KF968734	481	*L.scolaroi*	PNN	9896	KF967764	887	*L.bibronii*

Gene	Sample	Genbank	bp	Sp	Gene	Sample	Genbank	bp	Sp
CMOS	13034	KF968735	481	*L.scolaroi*	PNN	9999	KF967887	887	*L.sp.lineo*
CMOS	13039	KF968797	481	*L.zullyae*	PNN	10132	KF967873	887	*L.sp.1*
CMOS	13040	KF968798	481	*L.zullyae*	PNN	10391	KF967781	887	*L.darwinii*
CMOS	13050	KF968648	475	*L.chacabucoense*	PNN	10909	KF967840	887	*L.pseudoanomalus*
CMOS	13053	KF968753	478	*L.sp.lineo*	PNN	10926	KF967915	887	*L.wiegmannii*
CMOS	13055	KF968754	478	*L.sp.lineo*	PNN	10968	KF967926	928	*L.telsen*
CMOS	13067	KF968808	527	*L.senguer*	PNN	11103	KF967797	887	*L.inacayali*
CMOS	13120	KF968810	528	*L.boulengeri*	PNN	11246	KF967829	887	*L.morenoi*
CMOS	13134	KF968751	481	*L.sp.1*	PNN	11341	KF967796	887	*L.hermannunezi*
CMOS	13164	KF968686	481	*L.lentus*	PNN	11429	KF967928	950	*L.sp.4*
CMOS	14192	KF968672	481	*L.hermannunezi*	PNN	12006	KF967831	887	*L.multicolor*
CMOS	916862	KF968692	481	*L.lutzae*	PNN	12021	KF967836	887	*L.ornatus*
CytB	543	KF968823	705	*L.andinus*	PNN	12155	KF967871	887	*L.sp.1*
CytB	650	KF968960	694	*L.vallecurensis*	PNN	12284	KF967929	950	*L.inacayali*
CytB	1092	KF968827	705	*L.azarai*	PNN	12330	KF967932	927	*L.sitesi*
CytB	2034	KF968853	705	*L.famatinae*	PNN	12463	KF967848	887	*L.ruibali*
CytB	2178	KF968839	705	*L.cuyanus*	PNN	12555	KF967757	887	*L.andinus*
CytB	2200	KF968837	705	*L.canqueli*	PNN	12565	KF967778	887	*L.cuyanus*
CytB	2300	KF968904	705	*L.pseudoanomalus*	PNN	12699	KF967857	887	*L.scapularis*
CytB	2375	KF968912	705	*L.salinicola*	PNN	12772	KF967920	887	*L.wiegmannii*
CytB	2420	KF968970	705	*L.xanthoviridis*	PNN	12851	KF967758	887	*L.anomalus*
CytB	2431	KF968886	705	*L.melanops*	PNN	12928	KF967820	887	*L.martorii*
CytB	2548	KF968939	677	*L.rothi*	PNN	12967	KF967812	887	*L.loboi*
CytB	2561	KF968883	705	*L.martorii*	PNN	13013	KF967766	887	*L.boulengeri*
CytB	2644	KF968889	685	*L.melanops*	PNN	13033	KF967858	887	*L.scolaroi*
CytB	2698	KF968959	705	*L.vallecurensis*	PNN	13034	KF967859	590	*L.scolaroi*
CytB	2709	KF968850	705	*L.eleodori*	PNN	13039	KF967924	887	*L.zullyae*
CytB	3295	KF968876	705	*L.loboi*	PNN	13040	KF967925	887	*L.zullyae*
CytB	3485	KF968990	805	*L.boulengeri*	PNN	13050	KF967773	887	*L.chacabucoense*
CytB	3524	KF968991	805	*L.rothi*	PNN	13053	KF967878	887	*L.sp.lineo*
CytB	3610	KF968831	705	*L.boulengeri*	PNN	13055	KF967879	887	*L.sp.lineo*
CytB	4039	KF968966	705	*L.wiegmannii*	PNN	13067	KF967934	950	*L.senguer*
CytB	4040	KF968967	660	*L.wiegmannii*	PNN	13120	KF967936	950	*L.boulengeri*
CytB	4046	KF968855	705	*L.grosseorum*	PNN	13134	KF967876	887	*L.sp.1*
CytB	4159	KF968868	705	*L.koslowskyi*	PNN	13164	KF967808	887	*L.lentus*
CytB	4299	KF968964	594	*L.wiegmannii*	PNN	14192	KF967794	887	*L.hermannunezi*
CytB	4300	KF968965	705	*L.wiegmannii*	PNN	916862	KF967815	887	*L.lutzae*
CytB	4459	KF968957	705	*L.uspallatensis*	PNN	4464	KF967833	886	*L.Liolaemus*
CytB	4464	KF968892	705	*L.multimaculatus*	PRLR	2	KF967638	431	*L.multimaculatus*
CytB	4531	KF968881	705	*L.mapuche*	PRLR	15	KF967637	431	*L.multimaculatus*
CytB	5019	KF968849	705	*L.dorbignyi*	PRLR	543	KF967552	431	*L.andinus*
CytB	5076	KF968847	705	*L.donosobarrosi*	PRLR	544	KF967553	431	*L.andinus*
CytB	5461	KF968949	705	*L.tehuelche*	PRLR	650	KF967717	431	*L.vallecurensis*
CytB	5462	KF968950	705	*L.tehuelche*	PRLR	1092	KF967556	431	*L.azarai*
CytB	5530	KF968951	705	*L.telsen*	PRLR	1626	KF967675	431	*L.sp.1*
CytB	5531	KF968841	705	*L.sagei*	PRLR	2034	KF967588	431	*L.famatinae*
CytB	5753	KF968845	705	*L.cuyumhue*	PRLR	2178	KF967575	431	*L.cuyanus*
CytB	5759	KF968905	705	*L.puelche*	PRLR	2200	KF967567	431	*L.canqueli*
CytB	5761	KF968864	705	*L.josei*	PRLR	2284	KF967728	431	*L.xanthoviridis*
CytB	5763	KF968862	705	*L.josei*	PRLR	2300	KF967645	431	*L.pseudoanomalus*
CytB	6007	KF968885	705	*L.melanops*	PRLR	2369	KF967652	431	*L.ruibali*

Gene	Sample	Genbank	bp	Sp	Gene	Sample	Genbank	bp	Sp
CytB	6262	KF968992	805	*L.telsen*	PRLR	2375	KF967658	431	*L.salinicola*
CytB	6724	KF968880	705	*L.magellanicus*	PRLR	2420	KF967729	431	*L.xanthoviridis*
CytB	6877	KF968993	805	*L.telsen*	PRLR	2431	KF967625	431	*L.melanops*
CytB	6888	KF968909	705	*L.rothi*	PRLR	2548	KF967699	431	*L.sp.*
CytB	6911	KF968919	705	*L.sp.2*	PRLR	2561	KF967622	431	*L.martorii*
CytB	6914	KF968920	705	*L.sp.2*	PRLR	2596	KF967701	431	*L.sp.1*
CytB	7084	KF968833	705	*L.boulengeri*	PRLR	2644	KF967631	431	*L.melanops*
CytB	7206	KF968913	705	*L.sarmientoi*	PRLR	2698	KF967716	431	*L.vallecurensis*
CytB	7300	KF968867	705	*L.kolengh*	PRLR	2709	KF967584	431	*L.eleodori*
CytB	7471	KF968872	705	*L.lineomaculatus*	PRLR	2947	KF967569	431	*L.casamiquelai*
CytB	7953	KF968840	705	*L.josei*	PRLR	3295	KF967614	431	*L.loboi*
CytB	8426	KF968956	705	*L.uptoni*	PRLR	3524	KF967748	531	*L.rothi*
CytB	8693	KF968952	705	*L.telsen*	PRLR	3610	KF967563	431	*L.boulengeri*
CytB	8730	KF968910	705	*L.sagei*	PRLR	3690	KF967578	431	*L.cuyumhue*
CytB	9027	KF968996	805	*L.senguer*	PRLR	4039	KF967723	431	*L.wiegmannii*
CytB	9183	KF968934	705	*L.sp.1*	PRLR	4040	KF967724	431	*L.wiegmannii*
CytB	9190	KF968946	705	*L.sp.1*	PRLR	4046	KF967592	431	*L.grosseorum*
CytB	9202	KF968937	705	*L.sp.1*	PRLR	4155	KF967574	431	*L.cuyanus*
CytB	9205	KF968938	705	*L.sp.1*	PRLR	4159	KF967606	431	*L.koslowskyi*
CytB	9211	KF968998	795	*L.sp.4*	PRLR	4299	KF967718	431	*L.wiegmannii*
CytB	9221	KF968917	705	*L.silvanae*	PRLR	4300	KF967719	431	*L.wiegmannii*
CytB	9222	KF968918	677	*L.silvanae*	PRLR	4459	KF967715	431	*L.uspallatensis*
CytB	9238	KF968825	705	*L.archeforus*	PRLR	4464	KF967636	431	*L.multicolor*
CytB	9340	KF968852	705	*L.escarchadosi*	PRLR	4472	KF967703	431	*L.sp.1*
CytB	9388	KF968931	705	*L.sp.1*	PRLR	4473	KF967704	431	*L.sp.1*
CytB	9395	KF968830	665	*L.baguali*	PRLR	4530	KF967619	431	*L.mapuche*
CytB	9408	KF968948	705	*L.tari*	PRLR	4531	KF967620	431	*L.mapuche*
CytB	9454	KF968854	705	*L.gallardoi*	PRLR	4891	KF967589	431	*L.fitzingerii*
CytB	9489	KF968856	705	*L.hatcheri*	PRLR	5019	KF967583	431	*L.dorbignyi*
CytB	9618	KF968953	705	*L.tristis*	PRLR	5076	KF967581	431	*L.donosobarrosi*
CytB	9619	KF968954	705	*L.tristis*	PRLR	5135	KF967694	431	*L.sp.1*
CytB	9999	KF968944	705	*L.sp.1*	PRLR	5203	KF967591	431	*L.goetschi*
CytB	10391	KF968846	705	*L.darwinii*	PRLR	5461	KF967707	431	*L.tehuelche*
CytB	10909	KF968902	705	*L.pseudoanomalus*	PRLR	5462	KF967708	431	*L.tehuelche*
CytB	10926	KF968962	705	*L.wiegmannii*	PRLR	5530	KF967709	431	*L.telsen*
CytB	10968	KF968974	805	*L.telsen*	PRLR	5531	KF967654	431	*L.sagei*
CytB	11103	KF968861	705	*L.inacayali*	PRLR	5581	KF967573	431	*L.chehuachekenk*
CytB	11246	KF968890	705	*L.morenoi*	PRLR	5629	KF967572	431	*L.chehuachekenk*
CytB	11341	KF968860	705	*L.tromen*	PRLR	5753	KF967577	431	*L.cuyumhue*
CytB	12006	KF968893	705	*L.multicolor*	PRLR	5758	KF967646	431	*L.puelche*
CytB	12019	KF968894	705	*L.ornatus*	PRLR	5759	KF967647	431	*L.puelche*
CytB	12021	KF968895	705	*L.ornatus*	PRLR	5761	KF967601	431	*L.josei*
CytB	12284	KF968977	805	*L.inacayali*	PRLR	5763	KF967602	431	*L.josei*
CytB	12330	KF968980	805	*L.sitesi*	PRLR	5826	KF967681	431	*L.sp.1*
CytB	12565	KF968844	705	*L.cuyanus*	PRLR	6007	KF967629	431	*L.melanops*
CytB	12772	KF968969	705	*L.wiegmannii*	PRLR	6017	KF967630	431	*L.melanops*
CytB	12851	KF968824	705	*L.anomalus*	PRLR	6724	KF967618	431	*L.magellanicus*
CytB	12894	KF968896	614	*L.sp.1*	PRLR	6888	KF967651	431	*L.rothi*
CytB	12928	KF968882	705	*L.martorii*	PRLR	6911	KF967669	431	*L.somuncurae*
CytB	12967	KF968875	705	*L.loboi*	PRLR	6914	KF967670	431	*L.somuncurae*
CytB	13013	KF968836	705	*L.boulengeri*	PRLR	7084	KF967565	431	*L.boulengeri*

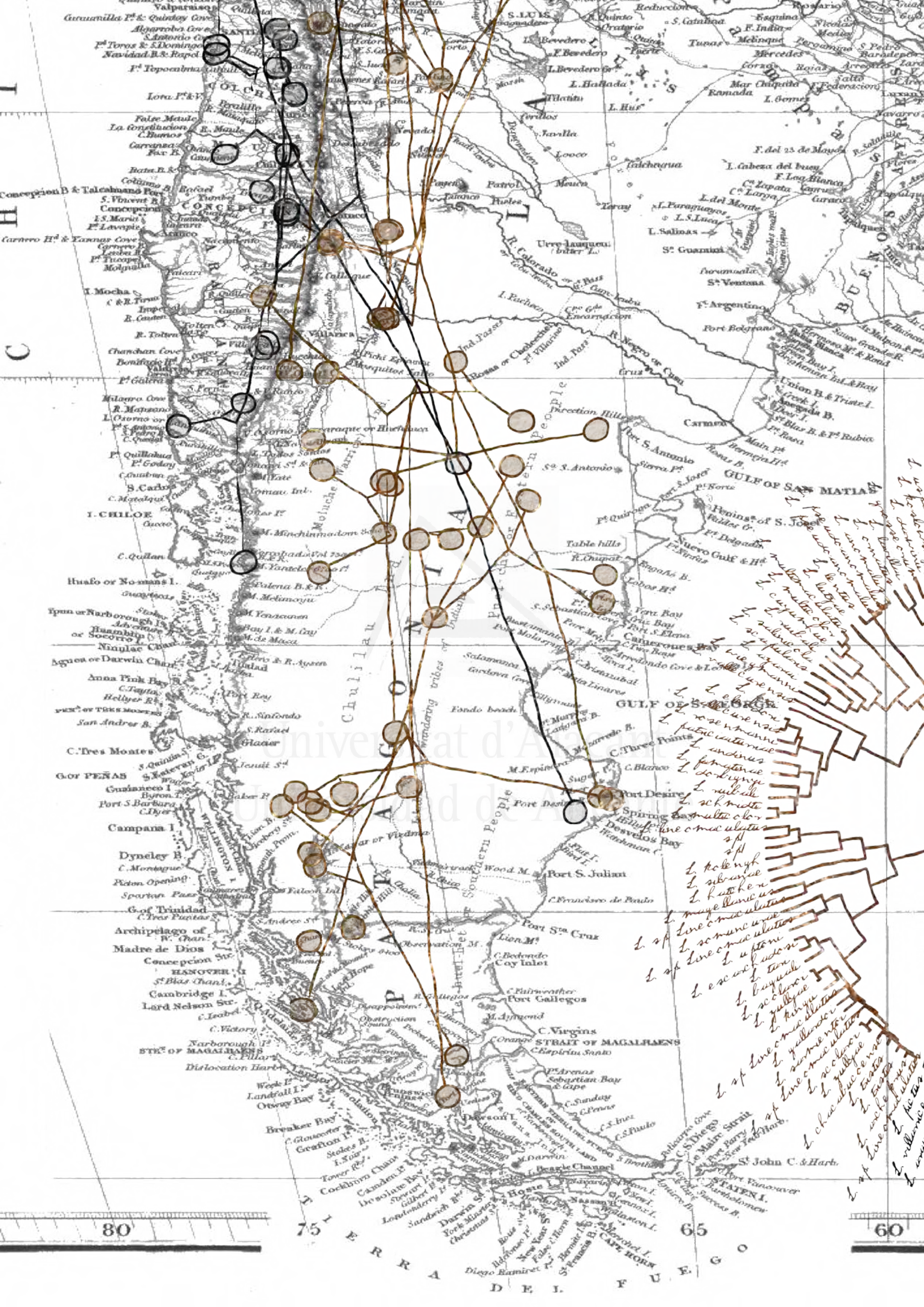
Gene	Sample	Genbank	bp	Sp	Gene	Sample	Genbank	bp	Sp
CytB	13033	KF968914	705	*L.scolaroi*	PRLR	7206	KF967660	431	*L.sarmientoi*
CytB	13039	KF968973	705	*L.zullyae*	PRLR	7300	KF967605	407	*L.kolengh*
CytB	13050	KF968843	705	*L.sp.5*	PRLR	7471	KF967611	431	*L.lineomaculatus*
CytB	13053	KF968941	705	*L.sp.1*	PRLR	7953	KF967603	431	*L.josei*
CytB	13055	KF968942	705	*L.sp.1*	PRLR	8323	KF967623	431	*L.martorii*
CytB	13067	KF968982	805	*L.senguer*	PRLR	8426	KF967713	431	*L.uptoni*
CytB	13120	KF968984	805	*L.boulengeri*	PRLR	8693	KF967710	431	*L.telsen*
CytB	13164	KF968871	705	*L.lentus*	PRLR	8730	KF967655	431	*L.sagei*
CytB	14192	KF968858	705	*L.hermannunezi*	PRLR	9027	KF967753	531	*L.senguer*
CytB	916862	KF968878	705	*L.lutzae*	PRLR	9183	KF967687	431	*L.sp.lineo*
CytB	LM2	KF968822	677	*L.multimaculatus*	PRLR	9190	KF967688	431	*L.sp.lineo*
cytochrome	1626	KF968926	705	*L.sp.1*	PRLR	9202	KF967689	431	*L.sp.lineo*
cytochrome	2596	KF968922	705	*L.sp.1*	PRLR	9205	KF967690	431	*L.sp.lineo*
cytochrome	9258	KF968924	705	*L.sp.1*	PRLR	9221	KF967667	431	*L.silvanae*
cytochrome	9277	KF968928	705	*L.sp.1*	PRLR	9222	KF967668	431	*L.silvanae*
cytochrome	9678	KF968925	705	*L.sp.1*	PRLR	9238	KF967555	431	*L.archeforus*
cytochrome	10132	KF968900	705	*L.sp.4*	PRLR	9258	KF967671	431	*L.sp.1*
cytochrome	11429	KF968976	805	*L.sp.4*	PRLR	9277	KF967673	431	*L.sp.1*
cytochrome	12155	KF968933	705	*L.sp.1*	PRLR	9340	KF967586	431	*L.escarchadosi*
cytochrome	13134	KF968929	705	*L.sp.1*	PRLR	9388	KF967691	431	*L.sp.lineo*
KIF24	9211	KF968259	534	*L.sp.4*	PRLR	9395	KF967559	431	*L.baguali*
KIF24	2	KF968147	465	*L.multimaculatus*	PRLR	9408	KF967706	431	*L.tari*
KIF24	15	KF968146	465	*L.multimaculatus*	PRLR	9454	KF967590	431	*L.gallardoi*
KIF24	326	KF968114	467	*L.kingii*	PRLR	9489	KF967593	431	*L.hatcheri*
KIF24	543	KF968064	465	*L.andinus*	PRLR	9618	KF967711	431	*L.tristis*
KIF24	544	KF968065	465	*L.andinus*	PRLR	9619	KF967712	431	*L.tristis*
KIF24	650	KF968221	465	*L.vallecurensis*	PRLR	9678	KF967674	431	*L.sp.1*
KIF24	1092	KF968070	465	*L.azarai*	PRLR	9999	KF967693	431	*L.sp.lineo*
KIF24	2034	KF968098	465	*L.famatinae*	PRLR	10132	KF967679	431	*L.sp.1*
KIF24	2200	KF968079	467	*L.canqueli*	PRLR	10391	KF967579	431	*L.darwinii*
KIF24	2284	KF968232	467	*L.xanthoviridis*	PRLR	10909	KF967644	431	*L.pseudoanomalus*
KIF24	2300	KF968154	465	*L.pseudoanomalus*	PRLR	10926	KF967721	431	*L.wiegmannii*
KIF24	2375	KF968164	465	*L.salinicola*	PRLR	10968	KF967734	531	*L.telsen*
KIF24	2420	KF968233	467	*L.xanthoviridis*	PRLR	11103	KF967598	431	*L.inacayali*
KIF24	2431	KF968136	467	*L.melanops*	PRLR	11246	KF967632	431	*L.morenoi*
KIF24	2548	KF968202	467	*L.sp.*	PRLR	11341	KF967597	431	*L.hermannunezi*
KIF24	2561	KF968133	298	*L.martorii*	PRLR	11429	KF967736	531	*L.sp.4*
KIF24	2596	KF968204	467	*L.sp.1*	PRLR	12006	KF967634	431	*L.multicolor*
KIF24	2644	KF968141	467	*L.melanops*	PRLR	12019	KF967639	431	*L.ornatus*
KIF24	2698	KF968220	465	*L.vallecurensis*	PRLR	12021	KF967640	431	*L.ornatus*
KIF24	2709	KF968094	465	*L.eleodori*	PRLR	12155	KF967677	431	*L.sp.1*
KIF24	3295	KF968125	467	*L.loboi*	PRLR	12284	KF967737	531	*L.inacayali*
KIF24	3485	KF968251	534	*L.boulengeri*	PRLR	12330	KF967740	531	*L.sitesi*
KIF24	3524	KF968252	534	*L.rothi*	PRLR	12463	KF967653	431	*L.ruibali*
KIF24	3610	KF968076	467	*L.boulengeri*	PRLR	12555	KF967554	431	*L.andinus*
KIF24	3690	KF968088	465	*L.cuyumhue*	PRLR	12565	KF967576	431	*L.cuyanus*
KIF24	4039	KF968227	465	*L.wiegmannii*	PRLR	12699	KF967662	431	*L.scapularis*
KIF24	4040	KF968228	465	*L.wiegmannii*	PRLR	12772	KF967726	431	*L.wiegmannii*
KIF24	4046	KF968102	465	*L.grosseorum*	PRLR	12928	KF967621	431	*L.martorii*
KIF24	4155	KF968085	467	*L.cuyanus*	PRLR	12967	KF967613	431	*L.loboi*
KIF24	4159	KF968116	465	*L.koslowskyi*	PRLR	13013	KF967562	431	*L.boulengeri*

Gene	Sample	Genbank	bp	Sp	Gene	Sample	Genbank	bp	Sp
KIF24	4299	KF968222	465	*L.wiegmannii*	PRLR	13033	KF967663	431	*L.scolaroi*
KIF24	4300	KF968223	465	*L.wiegmannii*	PRLR	13034	KF967664	431	*L.scolaroi*
KIF24	4459	KF968219	465	*L.uspallatensis*	PRLR	13039	KF967730	431	*L.zullyae*
KIF24	4464	KF968145	465	*L.multicolor*	PRLR	13040	KF967731	431	*L.zullyae*
KIF24	4472	KF968206	467	*L.sp.1*	PRLR	13050	KF967570	431	*L.chacabucoense*
KIF24	4473	KF968207	467	*L.sp.1*	PRLR	13053	KF967684	431	*L.sp.lineo*
KIF24	4530	KF968130	467	*L.mapuche*	PRLR	13055	KF967685	431	*L.sp.lineo*
KIF24	4531	KF968131	467	*L.mapuche*	PRLR	13067	KF967742	530	*L.senguer*
KIF24	4891	KF968099	452	*L.fitzingerii*	PRLR	13120	KF967744	531	*L.boulengeri*
KIF24	5019	KF968093	465	*L.dorbignyi*	PRLR	13134	KF967682	431	*L.sp.1*
KIF24	5076	KF968091	467	*L.donosobarrosi*	PRLR	13164	KF967610	431	*L.lentus*
KIF24	5135	KF968197	467	*L.sp.1*	PRLR	14192	KF967595	431	*L.hermannunezi*
KIF24	5203	KF968101	467	*L.goetschi*	PRLR	916862	KF967616	431	*L.lutzae*
KIF24	5461	KF968210	467	*L.tehuelche*	PRLR	3485	KF967747	523	*L.Liolaemus*
KIF24	5462	KF968211	467	*L.tehuelche*	PRLR	6262	KF967749	502	*L.Liolaemus*
KIF24	5530	KF968212	467	*L.telsen*	PRLR	6877	KF967750	510	*L.Liolaemus*
KIF24	5531	KF968160	467	*L.sagei*	PRLR	9896	KF967560	431	*L.Liolaemus*
KIF24	5581	KF968084	467	*L.chehuachekenk*					

Table S3. Species names and GenBank accession numbers of external species for time calibration.

Sp	12s	C-MOS	CYTB	PNN	PRLR	KIF24	MXMRA5
Acrochordus granulatus	AF544738	HM234057	AF217841	JN703047			
Agkistrodon contortrix			EU483260	JN703043	JN880801		
Agkistrodon halys			U65680				
Agkistrodon piscivorus		AF471096	AF471074				
Alligator mississippiensis	L28074	JF315210	AF159028	XM006268340	XM006270038	XM006269964	XM006277556
Anilius scytale	AF512729	AF544722	U69737	EU390953	JN880805		
Aspidoscelis tigris				EU390947	HQ130585		
Bipes canaliculatus	EU203658	FJ518700	AY605482	GU456066	JN880811		
Bitis arietans	EU852316		AJ275688		HM623448		
Caiman crocodilus	EU621799	JF315166	EU496845	JX533295			
Chalcides ocellatus	AY649106	JQ344216	FJ972228	JQ344238			
Chamaeleo calyptratus	NC_012420	HF570667	EF222192	GU456037	JN880819		
Charina trivirgata	AF544749	AF544687		EU390975			
Charina umbratica			KF811115				
Chilabothrus striatus		AY099966			JN880832		
Cnemidophorus tigris	AY046448	AF039481	AF006266				
Colobosaura modesta	AY218003	EU116677	AY217799	JN568342	JN880821		
Crotaphytus collaris	L40439	AY987985	EU037439	JF804496	JN880825		
Cylindrophis ruffus	AF512738	AF471133	AF471032	EU390962			
Elgaria multicarinata	AY649110	AF039479	AF361519	GU456044	JN880830		
Epicrates striatus		DQ465553	U69791	JN703049			
Eryx colubrinus		DQ465568	U69811	EU390966	JN880833		
Eunectes notaeus	AF368057	HQ399536	U69810				
Eumeces schneideri				JQ344243			
Eurylepis taeniolatus			JQ344291	JQ344247			
Exiliboa placata	AF512742	AY099973	AY099989	JN703054	JN880836		
Gongylophis colubrinus	AF544747	AF544716					
Heloderma suspectum	AF004473	AY487348	AB167711	GU456046	JN880842		
Lacerta agilis	AF149947	EF632267	AY616241		JX963018	JX962994	
Lacerta viridis	AJ001480	DQ097131	AM292928	GU456064			
Lampropeltis getula	AY122821	FJ627796	AF337153	EU390972	HQ130586		
Lanthanotus borneensis	AH005465	AY662564			JN880848		
Leiocephalus barahonensis	U39564	DQ119594		JF804504	JN880850		
Lepidophyma flavimaculatum	AB162908	DQ249070	EU116526	GQ850673	JN880852		
Lichanura trivirgata		AY099974	U69844				
Pelodiscus sinensis	JQ688040	FJ230869	AY583692	XM006117711	XM006116599	XM006122984	XM006112246
Pelomedusa subrufa	U40642	AF109208	FN645215				
Phrynosoma cornutum	DQ385390	AY987989	AY141087	KR359888	KR359874		
Platysaurus pungweensis		EU116686	DQ090884	JN568356	JN880867		
Plica plica	AF362520	EF615737	EF616028	JF804526	JN880885		
Polychrus marmoratus	AF338329	AY987983	AB266749	JF804517	JN880871		
Rhineura floridana	AY881084	AY444021	NC_006282	GU456067	JN880874		
Sceloporus graciosus	AF440090		KC853767	GQ464590	GQ896087		
Sceloporus grammicus	AF154130	AF039478			GQ896088		
Shinisaurus crocodilurus	HQ008865	AY099976	AY099995	GU456047	JN880877		

Sp	12s	C-MOS	CYTB	PNN	PRLR	KIF24	MXMRA5
Sphenodon punctatus	AF534388		AF442451	GU456036	HQ130579		
Takydromus sexlineatus	AF206589	EF632288	GQ142142	JF804524			
Tropidophis haetianus	FJ755181	AY099962	FJ755181	JN703033			
Varanus salvator	AF004511	AF435017	GU476594	EU390946	JN880894		
Xantusia vigilis	AY218042	EU116814	AY217840	EU390948	HQ130583		
Xenosaurus grandis		AY662567		GU456048	JN880898		


PATAGONIA
GULF OF SAN MATIAS
GULF OF S. GEORGE
STRAIT OF MAGALHAENS
TIERRA DEL FUEGO
80
75
65
60
L. multicolor
L. schmidti
L. sp lineomaculatus
sp
sp
L. kolengh
L. silvanae
L. hatcheri
L. magellanicus
L. sp lineomaculatus
L. somuncurae
L. sp lineomaculatus
L. uptoni
L. escarchadosi
L. tari
L. baguali
L. scolaroi
L. zullyae
L. kingii
L. sp lineomaculatus
L. gallardoi
L. sarmientoi
L. sp lineomaculatus
L. scolaroi
L. zullyae
L. chacabucoense
L. tristis
L. tristis
L. archeforus
L. sp lineomaculatus
L. fictus
L. villarricae

Chapter III

Capítulo III

Evolution of thermal traits in *Liolaemus* lizards

INTRODUCTION

One of the earliest observations in the light of evolution is that more closely related species tend to have more similar characteristics (Darwin 1856). This pattern of shared characteristics among related species is called phylogenetic signal (Blomberg and Garland 2002). If a species, or a group of species, maintains ancestral characteristics beyond what is expected by its evolutionary relatedness, then the appropriate term is phylogenetic conservatism (Losos 2008). The concept of phylogenetic conservatism is important to explain processes allopatric speciation, historical biogeography, and even species richness patterns (Wiens and Graham 2005; Romdal et al. 2013). Phylogenetic niche conservatism is also one of the key assumptions underlying projections of ecological niches in time or space (Peterson et al. 1999; Araújo and Peterson 2012), since the assumption is made that the relationship between species and the environment will remain constant in time. Notice that niche conservatism in the context of projections of ecological niches is often invoked to refer to the idea of stasis in realized niches rather than the fundamental niches (sensu Hutchinson 1957; for discussion see also Araújo and Guisan 2006). This dichotomy between conservatism of realized niches versus fundamental niches has generated confusion because there is no theoretical expectation for realized niches to remain constant through space and time (Araújo and Peterson 2012), while there is ample evidence of evolution of traits controlling for the fundamental niches (e.g. Johnston and Selander 1964, Maron et al. 2004, Phillips et al. 2006, Buswell et al. 2011).

The projection of niche models under climate change scenarios is a common approach to estimate the effect of climate change on species (Peterson et al. 2011). Approximations to the Hutchinsonian niche can be obtained by means of controlled measurements using physiological and behavioral properties to create models based in biophysical processes (e.g. Kearney and Porter 2004, Kolbe et al. 2010). However, those experiments are both slow and costly and with around 1.8 million of described species – and many others to be described– the methods that require a lot of empirical information for every species are unpractical for forecasting the effects of climate change on biodiversity. In contrast, another approach to construct niche models has been used for a wide range of organisms. In this called bioclimatic approach, species distributions are correlated with environmental variables to approximate the ecological requirements of the species (e.g. Araújo and Pearson 2005, Araújo and Guisan 2006). These models have been projected under future climate change scenarios for a large number of species (e.g. Araújo et al. 2011). Yet, this approach is likely to underestimate the true climatic tolerances of the species, as species distributions are inherently influenced by multiple determinants, both historical and ecological (Araújo and Guisan 2006). This is especially problematic for species with limited dispersal capabilities whose distribution is not in equilibrium with climate (Araújo and Pearson 2005).

There are three directions of species response to climate change: phenological, distributional or physiological (Bellard et al. 2012). Those responses can be the result of phenotypic plasticity or adaptive evolutionary responses. For instance, an evolutionary increase in thermal tolerances and/or thermal preferences could temper (compensate for) the reduction in activity time, which is predicted to have a major role in future extinctions of lizards (Sinervo et al. 2010), saving species from extinction. Although the general assumption is that climate change is much faster than microevolutionary processes (Hof et al. 2011), the question is whether those changes can happen fast enough to reduce the fitness loss to a level in which extinction can be avoided or the species will have to move following the conditions that allow their survival (Peterson 2011).

Since the proposal of the Phylogenetic Independent Contrasts method by Felsenstein 1985, there has been a development of phylogenetic comparative methods (e.g. Hansen 1997, Pagel 1997, 1999, Diniz-Filho et al. 1998, Blomberg et al. 2003). The new methods that involve more complex approaches have overpassed the original purpose of overcoming the problem of non-independence of comparisons between species. Comparative methods are evolutionary models per se (Harvey and Purvis 1991) allowing to make inferences about the underlying evolutionary processes that have shaped the phylogeny, and can also be used to study phylogenetic signals and niche conservatism (Cooper et al. 2010).

In this work, we take advantage of the advance of phylogenetic comparative methods to investigate the phylogenetic signal of thermal tolerances and body size of Chilean *Liolaemus* lizards as well as its interaction with climate. The use of a time calibrated phylogeny (Ferri -Yáñez et al. Chapter 2) allows us to estimate how fast those thermal traits can change, in order to infer whether evolutionary capabilities can buffer the effect of global warming in ectotherms or not. In addition, we propose the use of the phylogenetic signature of species traits to predict physiological traits in species for which they are unknown. In addition, we suggest that physiological information at different hierarchical levels is fundamental. Physiological plasticity may be important not only to deal with the increasing rate of environmental temperature increase, but also with the increasing unpredictability of climatic anomalies (Bozinovic et al. 2011). In this vein and again, adaptive physiological acclimatization, in the context of global warming, may work as a buffer to minimize the coupling of environmental temperature and body temperature (Gvoždík 2012). It will be useful to know whether increased environmental variation has selected for increased physiological plasticity. Thus, new approaches linking physiological ecology and evolutionary ecology to climate change may produce important results at different scales. A major outcome will be to provide a solid, mechanistic foundation for predictions about the probability of a life form's success in the face of global change.

MATERIALS AND METHODS

LIOLAEMUS SAMPLING AND MAINTENANCE

Fieldwork and laboratory measurements were carried out from 2010 to 2012. Sampling localities were selected to maximize both the climatic gradient in Chile (from Calama to Tierra del Fuego) and the number of species. For that, we consulted several Chilean herpetologists and ecologists for known locations of different *Liolaemus* species representing the taxonomic diversity of the group in the different environments through Chile. Sampling localities ranged in latitude from 22° to 53° South and in altitude from sea level to 4000 m a.s.l. (Figure 1). The southernmost population sampled was in northern Tierra del Fuego, where *L. magellanicus* was captured and the northernmost population in Calama (above the tropic of Capricorn) where *L. paulinae* was captured. The highest population sampled was

Figure 1. Sampling locations of *Liolaemus* in Chile.

in Salar de Pedernales, where *L. schmidti* was captured and several populations of *Liolaemus* were sampled at, or close to, sea level (no populations were sampled below sea level). We also found a species (*Liolaemus flavipiceus*) which was not previously recorded in Chile (See Appendix 5) and increased the distributional range of *Liolaemus patriciaiturriae* (see Appendix 6). We also used this data to clarify the taxonomical status of some species (see Appendix 7). Animals were captured using a nose or by hand and the cloacal temperature of active individuals was measured immediately using a T-type thermocouple thermometer (Digi-Sense®, ±0.1 °C). Animals were then placed individually in a fabric bag and brought to the laboratory at the Pontificia Universidad Católica de Chile in Santiago de Chile. All individuals were identified to the species level and any taxonomical and distributional uncertainty was further investigated and, if relevant, it was published (See Appendix 5, Appendix 6 and Appendix 7).

We used 310 individuals belonging to 37 species in this study. Animals were maintained individually or in couples (Male-female or female-female, to avoid intra male aggressions) in plastic terrariums of 35 X 50 X 40 cm with a substrate of sand. A 100W infrared lightbulb was placed in the corner of each container to allow the lizards to thermorregulate. Animals were maintained in a room kept at 20-25 °C and with a photoperiod of 12 hours.

Each terrarium had a petri dish with water that was filled every day. Animals were also fed every day ad libitum with live mealworms (Tenebrio molitor larvae) and the terrariums were sprayed with water daily.

LIOLAEMUS THERMAL LIMITS

Three measurements were taken to characterize the thermal range of the species: critical thermal maximum (CT_{max}), critical thermal minimum (CT_{min}) and preferred body temperature (PBT)(e.g. Angilletta Jr. 2009).

Treatment 1: Preferred Body Temperature

Following Labra and Bozinovic 2002, to perform the preferred body temperature measurements, we used a terrarium of 20 X 90 cm in which a 100 watt infrared bulb was placed at one of the ends and the other was left at room temperature. Sand was used as a substrate. Operative temperature was measured at both ends of the enclosure with hollow metallic molds with a t-type thermocouple in the interior connected to a thermocouple thermometer. This approach allowed estimating that temperatures in the gradient covered the range between 25 and 60 °C.

Each individual was placed in the gradient and left undisturbed for one hour. After that period, the animal was quickly captured and its cloacal temperature immediately measured every 30 minutes until we obtained 4 preferred body temperature measurements per individual.

Treatment 2: Critical Thermal Minimum

We used a protocol similar to that of Labra et al. (2009) to measure the CT_{min}. We taped a thin t-type thermocouple to the cloaca of the animal then the animal was placed in a transparent plastic container and placed in a fridge at -10 °C. The rigthing response (the capacity of the animal to return to the upright position after being laid on his back) was measured every minute by turning around the plastic container. When the righting response stopped, the temperature was annotated and the treatment stopped.

Treatment 3: Critical Thermal Maximum

To measure CT_{max}, a T-type thermocouple was taped in the lizard cloaca. The lizard was then placed in a round container of 25 cm radius and heated with a 100W infrared lightbulb. The animal was heated at a rate of 0.5 °C per minute, and the righting response was checked every minute by flipping the animal with a brush until a body temperature of 38 °C and every 20 seconds above that temperature. When the loss of righting response occurred, the temperature was annotated and the animal was immediately removed from the container, cooled down with ambient temperature water and allowed to recover.

MORPHOLOGICAL MEASUREMENTS

Snout vent length (±0.1 mm), tail length (±0.1 mm) and weight (±0.01 g) were measured in the laboratory after the arrival of the animals.

PHYLOGENETIC HYPOTHESIS AND TEMPORAL CALIBRATION

We used the time calibrated phylogeny explained in Chapter 2 to estimate the rate of trait evolution and to study the relation between phylogenetic relatedness, thermal traits and environmental variables. For that, we pruned the phylogenetic tree leaving only the Chilean species (37 species), for which we have measured thermal traits.

RATE OF TRAIT EVOLUTION

To estimate the rate of evolutionary change, first we fitted a Brownian motion model to the phylogeny and to each trait that we used to estimate the ancestral state on each node of the phylogeny.

We use the ancestral states to estimate the change in the trait for each branch between two nodes (the difference between the values of the trait in both nodes), and then the branch lengths between nodes (in millions of years) to estimate the rate of character change between nodes (change rate = character change / branch length). We calculated character change rates for field body temperatures (FBT), Preferred body temperatures (PBT), critical thermal minimum (CT_{min}) and critical thermal maximum (CT_{max}). As evolutionary rates tend to vary, and we are interested to learn how much did they vary, we calculated the mean and the maximum rate of character change for each case, and we also analyze how the change rates are distributed using Pearsons moments measure of kurtosis and Pearson's moment coefficient of skewness.

ENVIRONMENTAL VARIABLES

Selected climate variables (i.e., maximum temperature of warmest month, annual mean temperature, minimum temperature of coldest month and total annual precipitation) were downloaded from worldclim.org (Hijmans et al. 2005). In the absence of reliable species distribution maps or atlas data we extracted the values for all the locations where the specimens were found using the Geographic Information System Quantum Gis 2.0 (QGIS Development Team 2016) We calculated the average of each variable for all the locations of each species for further analyses.

PHYLOGENETIC ANALYSIS: PHYLOGENETIC EIGENVECTOR REGRESSION

We used Phylogenetic Eigenvector Regression (PVR, Diniz-Filho et al. 1998) to analyze the relationships among phylogeny, thermal and morphological traits and the environment. PVR partitions the total variation of the trait (T) into phylogenetic (P) and specific (S). With this method the R^2 value can be interpreted as a measure of phylogenetic signal as it expresses the ratio between the P component and the T component.

PVR starts extracting eigenvectors using a principal coordinate analysis (PcoA; Gower 1966, Sneath and Sokal 1973) from a pairwise distance matrix that describes the phylogenetic relationships between species, then using the eigenvectors to model trait variation with standard Ordinary Least Square regression (OLS). The R^2 of the OLS regression represents the amount of phylogenetic inertia in the dataset and the residuals represent the specific component (S-component), which can be used to measure the evolutionary correlation between two traits by correlating the S-components of independent PVR models (Martins et al. 2002; Diniz-Filho et al. 2012b). Eigenvectors in PVR are the coordinates of the species in the multivariate space expressing the variation in the phylogenetic hyperspace (Diniz-Filho et al. 1998).

It is important to select the correct number of eigenvectors should be used as predictors in the OLS regression; Although Diniz-Filho et al. 1998 initially proposed the comparison of the distribution of eigenvalues with a broken stick model, in a later study (Diniz-Filho et al. 2012a) they found that an iterative selection searching for low residual autocorrelation is a more optimized solution. In this approach, as new eigenvectors are added to the model, the residuals autocorrelation are calculated again and the search stops when a threshold is reached for Moran's I (set to 0.05) or for its statistical signifficance ($P \leq 0.05$). PVR can also perform, using the eigenvectors and the environmental variables a variance partition analysis estimating how much of the variation in the trait is related to the phylogeny, to the environmental variable or both.

We generate Phylogenetic Signal Representation (PSR) curves by building models sequentially increasing the number of eigenvectors and plotting their R^2 against the accumulated eigenvalues (Diniz-Filho et al. 2012a). Under a brownian motion model, there is a linear relation between interspecific divergence and time. Thus, we can expect that adding consecutively eigenvectors to a PVR will generate a linear relation between the number of eigenvectors and the R^2 of the OLS regression. The deviation of the PVR curve from linearity (expressed by the PSR area) expresses deviations from brownian motion, showing if the trait has been evolving faster (if PVR area < 0) or slower (if PVR area >0) than expected (Diniz-Filho et al. 2012b).

PROJECTING CHARACTERS TO OTHER SPECIES IN THE PHYLOGENY

To estimate the values of the traits in species for which we have only their position in the phylogeny and their geographical location (and therefore the environmental variables) we start performing the principal coordinate analysis and extracting the eigenvectors using the complete phylogeny. We then remove the species (and the respective coefficients) for which the traits were not measured, and we performed the rest of the PVR analysis on them (a stepwise eigenvector selection and a OLS regression including the selected eigenvectors and an environmental variable). Finally, we use the coefficients from the OLS regression to estimate the value of the trait on the species for which the trait was not measured (Figure 2). As an example, we apply this method to estimate the traits (FBT, PBT, CT_{min}, CT_{max}, Weight and SVL) for the species in our phylogeny for which any of those traits is not available and to all the species for the traits that show some phylogenetic innertia. Furthermore, we used 10 fold cross validation to estimate the prediction error for those traits.

RESULTS

LIOLAEMUS THERMAL MEASUREMENTS

FBT of active individuals averaged 32 ºC, and PBT averaged 35.6 ºC, mean CT_{min} was 7.4 ºC

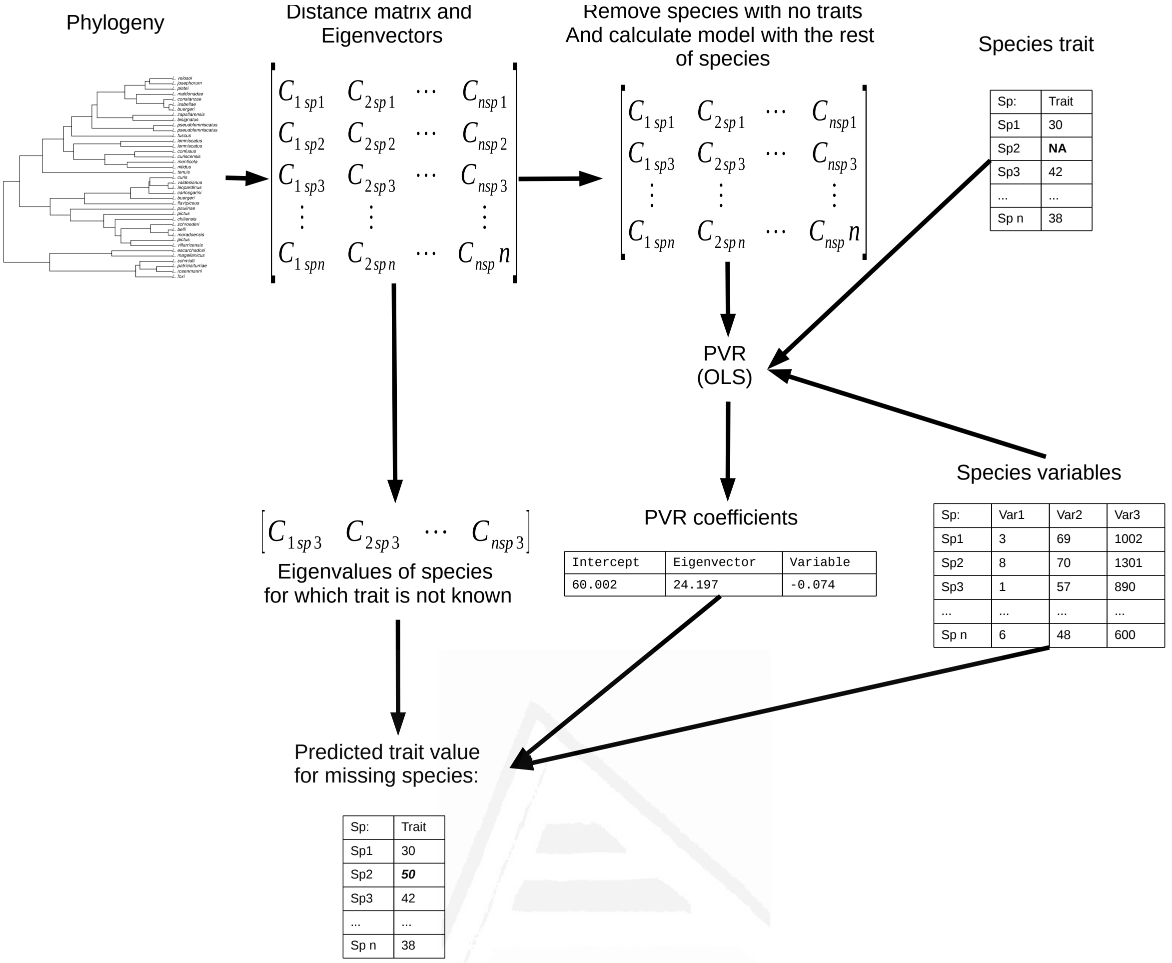


Figure 2. Conceptual framework for the prediction of traits based on phylogeny and environmental data.

and mean CT_{max} was 45ºC. As we already discussed elsewhere (Araújo et al. 2013) there is a striking difference in the intraspecific variability between CT_{min} and CT_{max}, and preferred body temperature lies in between (Table S1).

Rate of trait evolution

Average change rates for thermal traits are in the order of a few hundred thousandth of degree Celsius (1/100000) per century (Table 1), mean rates on morphological traits

Table 1. Mean and maximum rate of change for the measured traits. Thermal trait units are in degrees Celsius/century while Weight and SVL are in grams/century and mm/century respectively.

Trait (units)	Maximum rate	Mean rate	Kurtosis	Skewness
CT_{max}	0.000473	3.536 E-005	18.149452	2.326176
CT_{min}	0.000361	2.918 E-005	21.455788	-0.315957
PBT	0.000164	1.636 E-005	11.723817	1.088346
FBT	0.000388	4.44 E-005	10.303329	-0.796202
Weight	0.000982	0.000123	9.6326678	0.642074
SVL	0.00148	0.000223	8.027217	0.156704

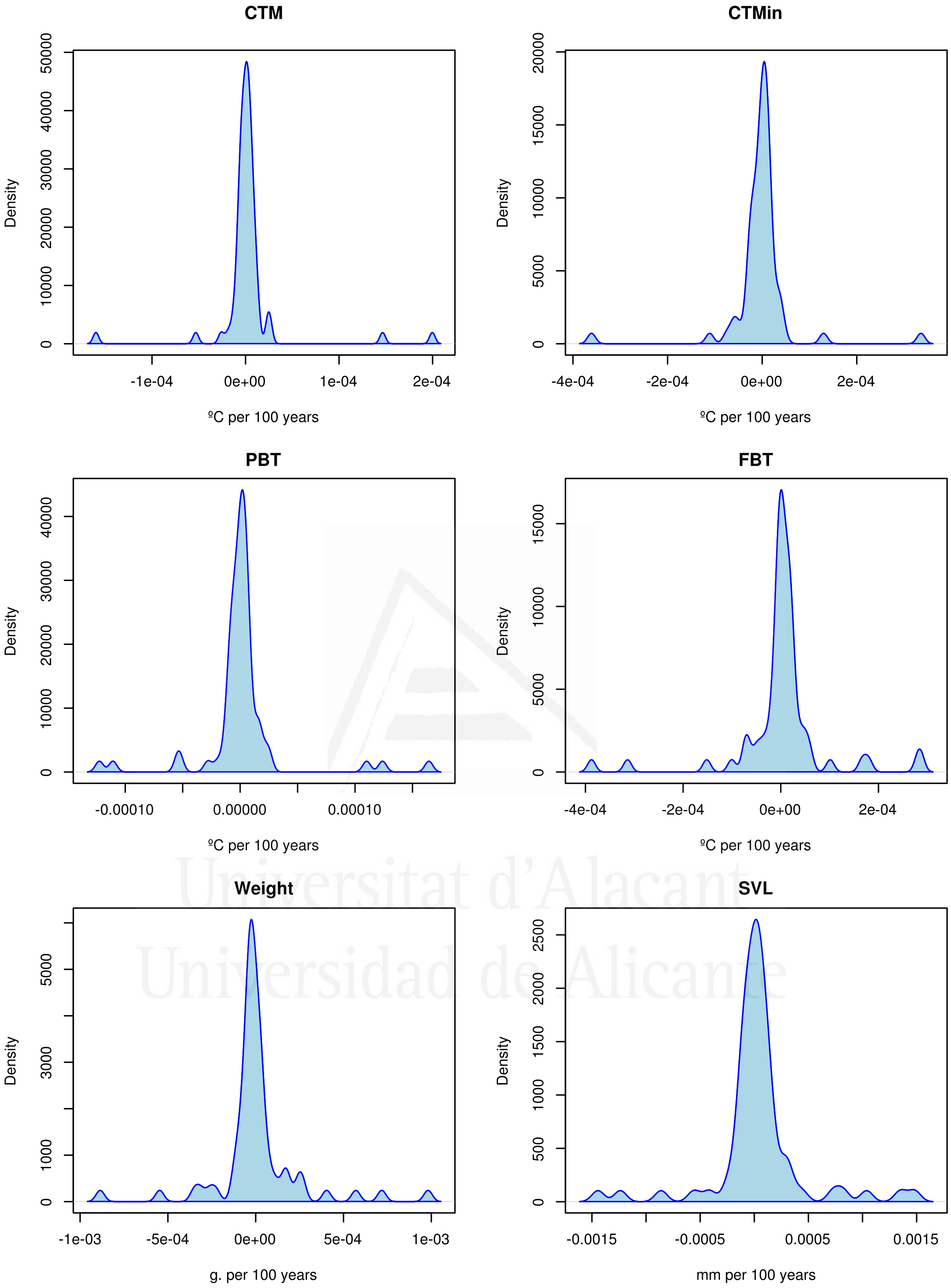


Figure 3. Density plots showing the distribution of trait change rates of branches in *Liolaemus* phylogeny.

(weight, SVL) are of few ten thousandth of grams and millimeters per century respectively. Maximum rates are close to one order of magnitude higher than average rates (Table 1). Pearsons moments measure of kurtosis, shows that the distribution of change rates are highly leptokurtic (strong, positive kurtosis), and so that those maximum rates depend on very few extreme values while almost all rates are much closer to zero (Table 1, Figure 3). Pearson's moment coefficient of skewness, on the other hand, shows that the distribution of change rates more or less symmetrical (Table 1).

INFLUENCE OF PHYLOGENY AND CLIMATE ON THERMAL AND MORPHOLOGICAL TRAITS

After using PVR to account for the effect of phylogenetic non-independence, several significant correlations between traits and between traits and environmental variables are apparent (Table 2). Field body temperature is positively correlated to CT_{min} and negatively to body size while preferred body temperature is positively correlated with CT_{max} and negatively with annual mean temperature. CT_{min} is negatively correlated with body weight and Precipitation and positively correlated with maximum temperature of warmest month. Body weight is negatively correlated with maximum temperature, although it is only marginally significant. Nevertheless, after adjusting for the possibility of spurious significance due to multiple correlations using a Bonferroni approach, only the relation between field body temperature and weight remained significant at the 95% confidence interval (see Table S4).

All PSR areas are negative only the PSR area of field body temperature is slightly higher (-0,1), although still negative (Figure 4). This is indicative of evolutionary rates that are slower than expected under the Brownian motion model, supporting the view that those traits are conserved to some degree.

The automated Eigenvector selection procedure systematically selected only one Eigenvector, which was either the first, second or third eigenvector (Table 3). For field body temperature, preferred body temperature and CT_{min} the second eigenvector was selected

Table 2. Phylogenetically corrected Pearson correlations and *P*-values between traits and between traits and environmental variables. Lower-left half matrix show the correlation coefficient and upper-right matrix shows the significance value. Numbers in bold in the upper left half-matrix highlight the significant values. Bold numbers in the lower-left matrix highlight the correlations that are still significant after applying a Bonferroni correction (see table S2 and S3)

	FBT	PBT	CT_{min}	CT_{max}	Weight	SVL	MaxTa	MeanTa	MinTa	Prec
FBT		0.808429	0.004479	0.069167	0.000002	0.001667	0.055501	0.180321	0.44013	0.96575
PBT	0.043877		0.205146	0.007705	0.844602	0.114815	0.117768	0.012479	0.08686	0.087435
CTMin	0.489336	-0.222884		0.32425	0.007712	0.32425	0.002501	0.149335	0.978241	0.045769
CTMax	0.320313	0.442937	0.177066		0.28175	0.11449	0.7395	0.786872	0.214396	0.115966
Weight	-0.715670	-0.034911	-0.455602	-0.190020		0.1739	0.049777	0.083424	0.40974	0.956648
SVL	0.518846	0.275480	0.177066	0.275718	-0.235146		0.609161	0.439658	0.316737	0.694514
MaxTa	0.331455	-0.269269	0.501745	-0.058274	-0.334151	-0.089497				
MeanTa	0.235328	-0.417939	0.252699	0.047397	-0.296764	-0.134923				
MinTa	0.136888	-0.293660	0.004859	0.215210	-0.143838	-0.174261				
Prec	-0.007650	0.293149	-0.344879	0.270548	0.009535	-0.068805				

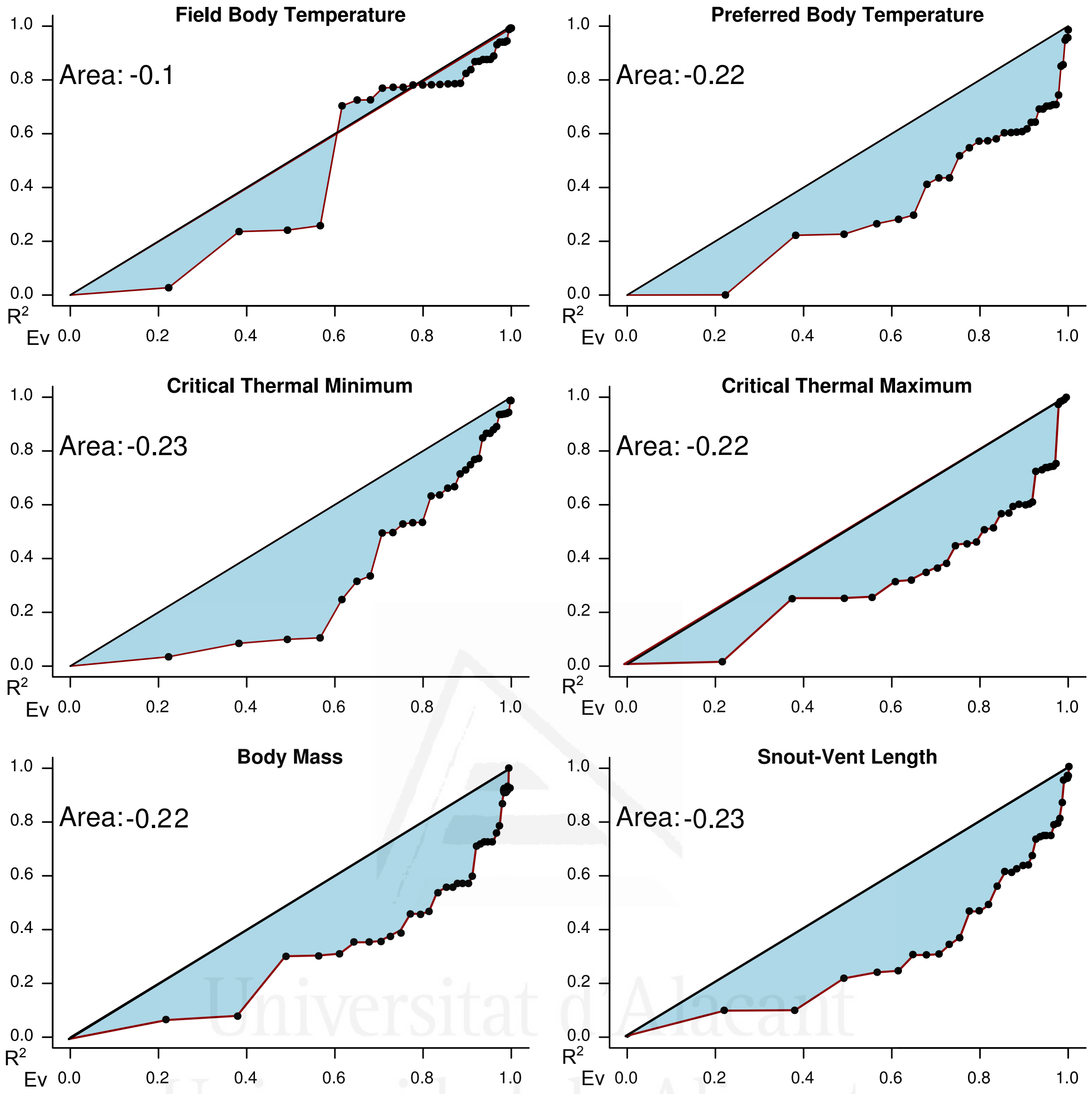


Figure 4. Phylogenetic Signal Representation curves for the six traits used in this work. X axis represents the sorted eigenvectors and y axis the R^2 of models fitted with increasing number of eigenvectors. The PSR area, representing the deviation from a Brownian motion evolutionary pattern is depicted in blue and summarized in the upper left area of each panel.

and for CT$_{max}$ and snout-vent length the first eigenvector was selected while the third eigenvector was selected for Weight.

P-values are only significant at 0.05 levels for field body temperature, preferred body temperature and Weight (Table 3), for which also adjusted R^2 is in general higher than for the rest of the traits.

The variance partition shows that the phylogenetic component (c) (Table 3, Figure 5) explains more of the variation in the trait than each independent environmental variable (a) for field body temperature and for preferred body temperature and that the overlap between the environmental and the phylogenetic variation was generally small. For thermal limits, both the phylogenetic and environmental component explain very little of the variation.

Table 3. Summary statistics for Phylogenetic Eigenvector Regression models including environmental variables. Column "Trait" represents the traits (thermal or morphological) used in each model, column "EnvVar" represent the environmental variable used in each model. Column "Vector" represent the Eigenvector selected by the stepwise algorithm for each model (note that the algorithm has only selected one eigenvector for each model, although it could have selected more than one). MoransI and M.*P*-val represent the value of Morans'I and the *P*-value for the eigenvector selection. R^2 and *P*-val show the regression coefficient and the significance of the model. Finally columns a, b, c and d show the fractions of the variation partition as proposed by Desdevises et al 2003: column a shows the proportion variation in the trait attributed solely to the environmental variable, b shows the proportion of variation in the trait attributed to both the environmental variable and phylogeny, c shows the proportion of variation attributed solely to the phylogeny and d shows the proportion of unexplained variation.

Trait	EnvVar	Vector	MoransI	M.*P*-val	R^2	*P*-val	a	b	c	d
FBT	MaxTa	c2	-0.0360	0.4600	0.3375	0.0456	0.1279	0.1168	0.0928	0.6625
FBT	MeanTa	c2	-0.0360	0.4600	0.2786	0.0052	0.0691	-0.0007	0.2103	0.7214
FBT	MinTa	c2	-0.0360	0.4600	0.2440	0.0063	0.0344	0.0002	0.2094	0.7560
FBT	Prec	c2	-0.0360	0.4600	0.2185	0.0071	0.0089	0.0004	0.2091	0.7815
PBT	MaxTa	c2	-0.0235	0.4515	0.2718	0.0016	0.0495	-0.0474	0.2696	0.7282
PBT	MeanTa	c2	-0.0235	0.4515	0.3177	0.0025	0.0955	-0.0065	0.2288	0.6823
PBT	MinTa	c2	-0.0235	0.4515	0.2732	0.0034	0.0509	-0.0054	0.2276	0.7268
PBT	Prec	c2	-0.0235	0.4515	0.2718	0.0274	0.0496	0.1007	0.1216	0.7282
CT_{min}	MaxTa	c2	-0.0290	0.8732	0.2874	0.7384	0.2341	0.0507	0.0026	0.7126
CT_{min}	MeanTa	c2	-0.0290	0.8732	0.1546	0.1783	0.1013	0.0016	0.0517	0.8454
CT_{min}	MinTa	c2	-0.0290	0.8732	0.0624	0.1967	0.0091	0.0007	0.0526	0.9376
CT_{min}	Prec	c2	-0.0290	0.8732	0.1975	0.0317	0.1442	-0.0778	0.1311	0.8025
CT_{max}	MaxTa	c1	-0.0257	0.1481	0.0597	0.5766	0.0264	0.0240	0.0093	0.9403
CT_{max}	MeanTa	c1	-0.0257	0.1481	0.1093	0.9789	0.0759	0.0333	1.986E-5	0.8907
CT_{max}	MinTa	c1	-0.0257	0.1481	0.1418	0.9807	0.1085	0.0333	1.595E-5	0.8582
CT_{max}	Prec	c1	-0.0257	0.1481	0.0341	0.3911	0.0008	0.0105	0.0228	0.9659
Mass	MaxTa	c3	-0.0312	0.8249	0.3218	0.0034	0.0866	0.0225	0.2127	0.6782
Mass	MeanTa	c3	-0.0312	0.8249	0.3565	0.0092	0.1212	0.0805	0.1547	0.6435
Mass	MinTa	c3	-0.0312	0.8249	0.4176	0.0120	0.0823	0.0841	0.1512	0.6824
Mass	Prec	c3	-0.0312	0.8249	0.2703	0.0020	0.0351	-0.0240	0.2593	0.7300
SVL	MaxTa	c1	-0.0295	0.9919	0.1839	0.4191	0.0894	0.0775	0.0171	0.8161
SVL	MeanTa	c1	-0.0295	0.9919	0.1960	0.6929	0.1014	0.0906	0.0040	0.8040
SVL	MinTa	c1	-0.0295	0.9919	0.1537	0.4104	0.0591	0.0762	0.0184	0.8463
SVL	Prec	c1	-0.0295	0.9919	0.0946	0.1040	8.3391	0.0153	0.0792	0.9054

Finally the effect of the environmental variables tends to be smaller than that of phylogeny for field and preferred body temperatures, while it tends to be larger (although also very small) for thermal limits. An exception to this pattern is the effect of maximum temperature of warmest month which has a relatively strong influence on CT_{min}. There is also a mixed effect of phylogeny and temperature related environmental variables on body size.

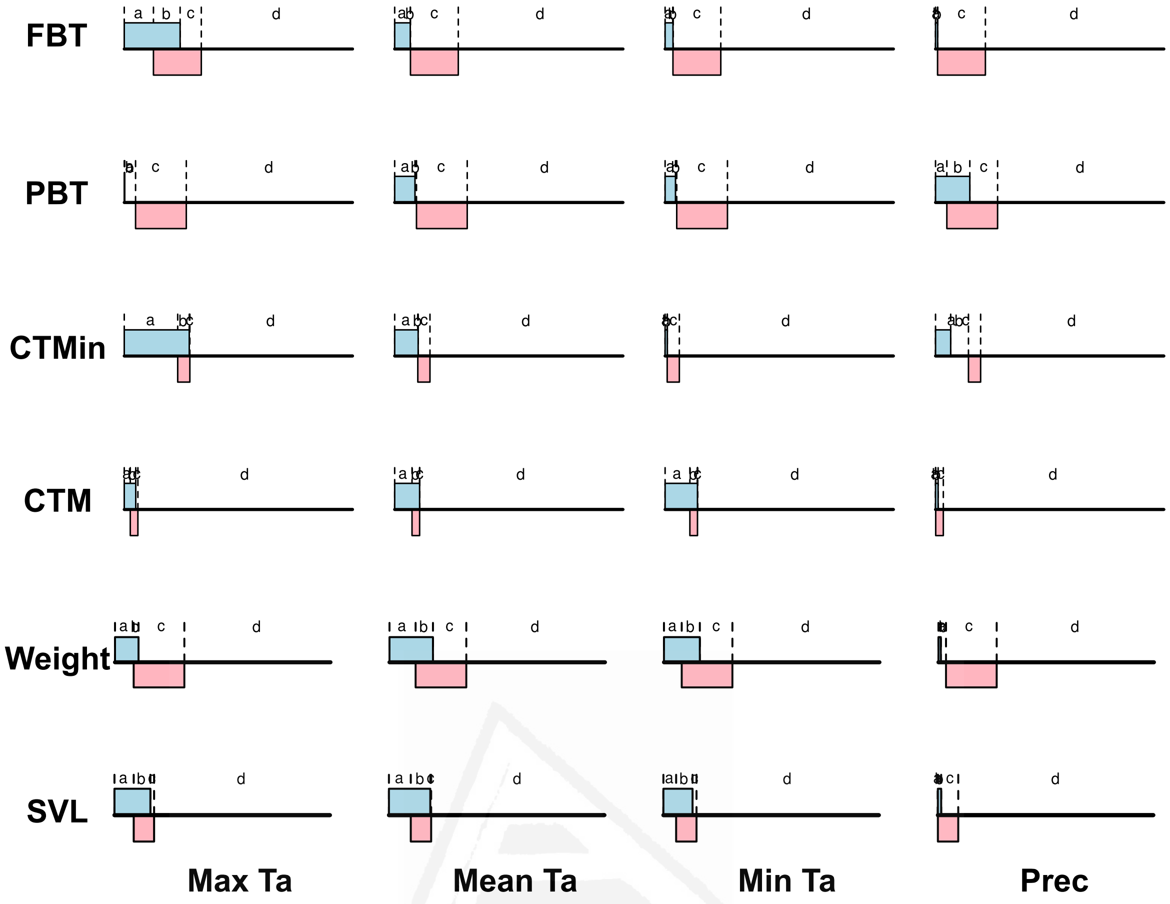


Figure 5. Variance partition representation for models with different variables and traits as in Desdevises 2003. Each column corresponds to one environmental variable and each row to a different trait. In each graph a shows the proportion variation in the trait attributed solely to the environmental variable, b shows the proportion of variation in the trait attributed to both the environmental variable and phylogeny, c shows the proportion of variation attributed solely to the phylogeny and d shows the proportion of unexplained variation. The blue rectangle represent all the variance related to the environmental variable and the pink rectangle all the variance related to phylogeny.

Overall, the PVR models explain between 25 to 35% of the variance of field and preferred body temperature and weight and between 5 to 20% of the variance in thermal limits and snout-vent length.

PROJECTING CHARACTERS TO OTHER SPECIES IN THE PHYLOGENY

We used the information from the eigenvectors to predict trait values for the species in which those were not measured. There was considerable variation in the predicted values of the thermal traits (of up to 4 ºC for field body temperature) depending on the environmental variable used as a co-predictor (Table 4). For field and preferred body temperature, we projected the PVR model and estimated the overall mean square of prediction error by performing a 10 fold cross validation (Figure 6, Table 5). The differences between predicted and measured trait values (the residuals) are much higher for extreme values

Table 4. Estimated values of traits predicted using PVR and the four different environmental variables. The value has been estimated for species for which one or several of the variables could not be measured for whatever reason. Continues in right the page.

Sp.	FBT				PBT				CT_{min}			
	MaxT	MeanT	MinT	Prec	MaxT	MeanT	MinT	Prec	MaxT	MeanT	MinT	Prec
L. villarricensis	33.00	34.07	31.49	32.70	37.61	36.77	35.92	35.71	6.94	7.67	7.76	5.09
L. confusus	34.55	33.19	30.18	32.88								
L. maldonadae	34.74	34.82	30.83	33.78								
L.valdesianus					37.59	36.73	35.90	35.67	8.54	7.79	7.70	6.25
L. pseudo.									6.87	6.61	7.15	7.18

Table 5. Shapiro normality test for the residuals of the projected traits and overall mean square of prediction of cross validation for FBT and PBT. W: Shapiro test statistic, *P*-val: signifficance value for the Shapiro test. Var: variance of the projected values. R^2: Adjuster R^2 between the projected and measured values for the species. SE: overall mean square of prediction of cross validation.

Trait	FBT					PBT				
	W	*P*-val	Var	R^2	SE	W	*P*-val	Var	R^2	SE
MaxT	0.878	0.001	14.835	0.581	21.55	0.984	0.878	0.890	0.521	0.96
MeanT	0.859	0.000	16.152	0.528	23.58	0.986	0.933	0.834	0.564	0.92
MinT	0.833	0.000	17.453	0.470	24.98	0.988	0.966	0.888	0.523	0.98
Prec	0.826	0.000	17.500	0.467	25.82	0.984	0.874	0.890	0.521	0.94

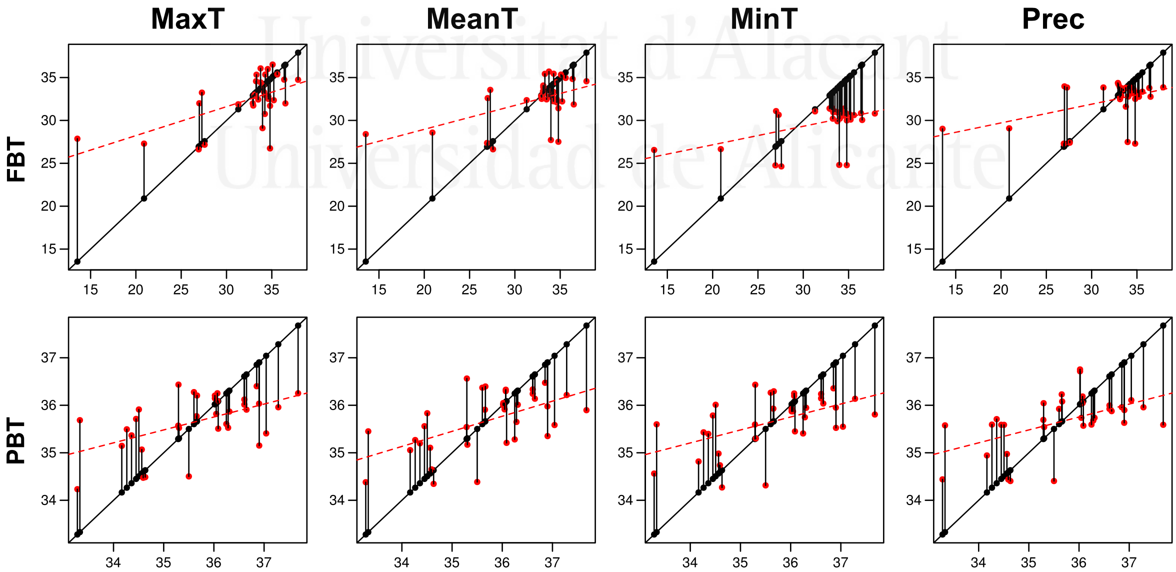


Figure 6. Projection of FTB and PBT values on the species in the phylogeny. Black dots along the 1-1 diagonal represent the measured values plotted against themselves. Red dots represent the reconstructed values (y axis) against the measured values (x axis). Vertical lines connect the predicted value and its measured par. Red dashed line repesents the regression line of the predicted values against the measured values.

Table 4. Continuation of Table 4.

Sp.	CT_{max}				SVL				Weight			
	MaxT	MeanT	MinT	Prec	MaxT	MeanT	MinT	Prec	MaxT	MeanT	MinT	Prec
L. villarricensis	44.90	46.42	47.94	44.08	53.62	53.51	51.17	55.68	15.87	15.77	14.34	21.42
L. confusus												
L. maldonadae					62.67	58.39	58.60	65.47	0.19	-2.76	1.35	3.93
L.valdesianus	46.83	46.98	47.75	44.45								
L. pseudo.												

of the measured trait (Figure 6). The normality test shows that residuals are not normally distributed for the projected FBT but the hypothesis of non-normality can be rejected for PBT (Table 5), the variance of the residuals is much higher for FBT than for PBT although the correlation between measured and estimated values are similar, somewhat higher for PBT (Table 5). Finally, the overall mean square of prediction of cross validation is much higher for FBT than for PBT.

Discussion

Climate change and evolutionary adaptation in *Liolaemus*

The increase in global temperatures during the 20th century and the projected rise for the 21st century (IPCC 2013), is several orders of magnitude faster than the highest measured change rate in any of the traits examined in this work. In other words, to match the current rate of temperature increase, the lizards would have to evolve around 100,000 times faster than the normal evolutionary rate of those traits and around 10,000 times faster than the maximum trait change rate measured here. In addition, the area under the phylogenetic signal representation curves show that the traits seem to be conserved beyond a Brownian motion model for Chilean *Liolaemus*. This suggests that physiological adaptation to climate change would require evolutionary rates that seem unprecedented in the history of the clade. The question then is if such an increase in evolutionary rate is realistic or evolutionary adaptation can be ruled out as mechanism to cope with climate change (e.g. Pörtner et al. 2006, Bozinovic and Pörtner 2015).

The slow rates of evolution found here contrast with recent finding of changes in thermal breath in range shifting species during current climate change (Lancaster et al. 2015) in which local adaptation of CT_{min} and thermal selection release for CT_{max} have increased thermal breadth. Nevertheless, those effects could be due to temperature acclimation rather than genetic change as CT_{min} is more responsive to acclimation (e.g. Kingsolver and Huey 1998, Clusella-Trullas and Chown 2013) than CT_{max}. Other cases that imply evolution happening in historical time scales refer to invasive species. House sparrows for instance, have developed morphological and coloration changes in areas where they were introduced in the nineteen century (Johnston and Selander 1964), cane toads in Australia are developing longer limbs, allowing them more mobility in the invasion front (Phillips et al. 2006). Also rapid evolution seems to be the norm rather than the exception for morphological characters in introduced plants in Australia (Buswell et al. 2011). On the other hand, there are little demonstrated cases of genetic change linked to Climate change (Gienapp et al. 2008). The examples of rapid evolution common on species introduced in novel environments where not only climate but also most biotic interactions have been replaced. Although it is an issue that requires further study, long time established biotic interactions may constrain evolution favoring conservatism (Wiens et al. 2010). The capacity of species to evolve with climate change may then depend on how it will affect those biotic interactions. In our case, *Liolaemus* could adapt to climate change by increasing CT_{max}, but variability of upper thermal tolerances is very low in our data, and is conserved across terrestrial plants and animals (Sunday et al. 2012; Araújo et al. 2013). Thermal acclimation could also help rise thermal limits and cope with climate change, but the capacity for upper thermal acclimation is low (Clusella-Trullas and Chown 2013). Lizards could also increase thermal preferences, which would increase potential activity time in a warmer environment (Sinervo et al. 2010; Gvoždík 2012), but critical thermal maxima in iguanids is coevolved with optimum temperatures (Hertz et al. 1993) and we found a correlation between CT_{max} and PBT (Table 2), so increasing thermal preferences may bring body temperatures dangerously close to CT_{max} (Sinervo et al. 2010) and lower performance.

On the one hand, our evolutionary estimates are averages rates between nodes, so if the change rate was not constant between nodes, higher evolutionary rates would have happened. Also, there is always an uncertainty in both the topology and the branch length of the phylogeny (see Chapter 2, Figure 2) and in the ecophysiological measurements. This uncertainty can vary our estimates and (although not necessarily) mean an increase of evolutionary rate. Also, the Brownian model used to predict the ancestral states tends to place those at the midpoint of the range values of the species. If the environment has been changing during the diversification process of the group, it is possible that this assumption is not true. Actually, global temperatures (Zachos et al. 2008), local climates and orography (Fiorella et al. 2015) have been changing profoundly since the start of the diversification of *Liolaemus* (see chapter 2 Figure 3), making this plausible. On the other hand, the oldest fossil evidence attributed to *Liolaemus* was found in the Patagonia region (Albino 2008, 2011) suggesting a more poleward distribution of the genus during warmer times. Finally, our results are in accordance with Quintero and Wiens 2013 who found for non-marine vertebrates, using time calibrated phylogenies for sister species, that realized niches evolved at an approximately similar rate as we have estimated for our data. This makes us conclude that significant evolutionary adaptation of physiological tolerances to climate change is very unlikely in the next decades.

PHYLOGENETIC STRUCTURE AND RELATION BETWEEN TRAITS AND CLIMATE

PVR analysis shows several relationships between traits that are independent of phylogenetic relations.

The strongest correlation found between traits is between field body temperature and body weight (-0.716), this negative correlation can indicate that the cost of thermoregulating in larger lizards may be increased due to they have lower heating rates (O'connor 1999; Ashton and Feldman 2003), so in a costly environment for thermoregulation bigger organisms would be forced to cope with lower (and more suboptimal) body temperatures. Also, there is a significant although weak negative relation between weight and maximum temperature of warmest month. Ashton and Feldman 2003 found that squamate species tended to intraspecifically increase their body size with increasing temperature (a reversed Bergman rule), the pattern found between maximum temperature of warmest month and Weight indicates that the relation could be extended to the interspecific level. Nevertheless, neither Pincheira-Donoso et al. 2007, Pincheira-Donoso et al. 2008 or Labra et al. 2009 found a clear interspecific pattern, although they used SVL as a measure of size and in our study the result is significant for body weight but not for SVL.

Field body temperature is significantly related to CT_{min}. On the other hand preferred body temperature, is significantly related to CT_{max} (but not to CT_{min} agreeing with Labra et al. 2009). Both field body temperatures and CT_{min} are the traits that are more related with climate in contrast to Labra et al. 2009 who did not find any relation between climate and CT_{min}. Field body temperature should be constrained by weather and climate, reflecting the stochasticity of sampling weather conditions, as there is a cost associated with thermoregulatory behavior that is dependent on habitat and climate (see Hertz et al. 1993, Angilletta et al. 2003). Preferred body temperature on the other hand, is measured in absence of thermoregulatory constrains and is much closer to CT_{max} than to CT_{min}, therefore decreasing the distance between PBT and CT_{max} can increase the risk of overheating. Also increasing it would reduce performance as PBT is close to optimum sprint performance in *Liolaemus* (Rodríguez-Serrano et al. 2009; Kubisch et al. 2011). Sinervo et al. 2010 found a Phylogenetic correlation between body temperature and CT_{max}. He also found a correlation between preferred and field body temperatures for *Sceloporus*, which he used to argue for using field instead of preferred temperatures in his extinction model. We did not find that pattern in our *Liolaemus* dataset which questions the use of that relation for his global model of extinction as the relation between field and body temperature may not be ubiquitous. Also, CT_{min} appears negatively related to Weight consistent with Labra et al. 2009 and with MaxTa, which supports the results of Cruz et al. 2005 who found that CT_{min} of Argentinian *Liolaemus* was negatively related with latitude.

The relationship between field body temperature and weight mentioned above, was not significant before applying the phylogenetic correction but using PVR to remove the effect of phylogeny resulted in a strong negative correlation. Phylogenetic comparative methods were firstly developed to allow independent comparisons between species as stated by Felsenstein 1985 and so avoiding type 1 errors due to phylogenetic relatedness. The expectation, then, and a common outcome is that correlations that may be observed between variables may weaken or become insignificant when applying a phylogenetic correction

(Garland et al. 2005). Nevertheless, the incorporation of phylogeny in the comparative analyses can also help clarify patterns across species (Garland 2001). In our study we have observed cases in which significant correlations between traits have only appeared when applying the phylogenetic correction (the case of the correlation between weight and field body temperature, See Table S2 and Table 2). This shows that phylogenetic autocorrelation can produce spurious correlations, but it can also mask the relationships between variables (and therefore create a false negative) which is then revealed when the effect of phylogeny is removed. It is then important not to discard an alternative hypothesis before accounting for phylogenetic effects.

Thermal limits show very little phylogenetic signal (Table 3, Figure 5) to the point that R^2 was not significant for thermal limits and SVL. In contrast, the remaining traits show some degree of phylogenetic structure. The variance partitioning also shows that the influence of the chosen environmental variables is generally small and also smaller than that of the phylogeny (Table 3, Figure 5). Even though, according to the PSR curves, all traits seem to evolve slower than it would be expected by only Brownian motion (Figure 4). The strong conservatism of upper thermal limits lack of phylogenetic signal raises the question of how informative and critical are thermal limits for the adaptation of species to heat, as CT_{max} varies very little and the relation of CT_{min} with the environment seems weak (except for Maximum temperature, although the model is non significant), in comparison to less extreme measures such as temperature preferences. Field body temperature shows a similar pattern as preferred body temperature, although both variables are not highly correlated with each other.

It is surprising the small influence of the environmental component in the CT_{min}, although there is some effect with Maximum temperature of warmest month, as previous works indicate a large scale relation between cold tolerance and latitude (Sunday et al. 2012). On the other hand, CT_{min} is a measure that has more intraspecific as well as interspecific variability. Also, CT_{min} shows more phenotypic plasticity (Hoffmann et al. 2013) which can add noise and obscure general patters. Nevertheless the contribution of maximum temperature of warmest month to the PVR model is relatively high (Table 3, Figure 5) although non signifficant.

USING PVR TO PREDICT TRAIT VALUES:

EXPANDING THE USE OF COMPARATIVE METHODS

The assessment of the effects of climate change on biodiversity requires large amounts of data for as many species as possible. Information on traits like thermal or hydric limits can improve forecasts of climate change effects (Buckley and Kingsolver 2012), nevertheless this kind of data is costly to obtain and, for a great number of species, unfeasible. This is one of the reasons why the use of process based models and biophysical models have not been applied often at large scale (Dormann et al. 2012). A way to address this problem is to find a way to reliably estimate those traits in non measured species. Our results show how this can be done using phylogenetic information and PVR, which allow also to incorporate environmental variables as covariates. Our analysis with FBT and PBT show that it can do so with a reasonable performance even though the phylogenetic signal is moderate (Table 5, Figure 6). Other phylogenetic comparative methods can be used to estimate trait values with different evolutionary models and the decision of which one to use opens an area for study and debate.

The increasing availability of large scale phylogenies (e.g. Pyron and Wiens 2011, Pyron et al. 2013, Prum et al. 2015) and the ready available information of atlas and climate data for for large groups of organisms (e.g. IUCN, Holt et al. 2013) allows using evolutionary models and comparative methods to estimate trait values for less known or rare species, which could greatly improve predictive models for the forecast of environmental change on biodiversity.

CONCLUDING REMARKS

Five conclusions can be drawn from these results: 1) climate change is several orders of magnitude faster than the fastest evolutionary rate detected for thermal traits, this rate is in agreement with the rate measured for estimated realized niches, 2) thermal physiological traits have varying degrees of correlation between them and with environmental variables, 3) Comparative methods can avoid type 1 errors but also type 2 errors, showing up patterns that are obscured by the phylogenetic relations, 4) thermal traits show little phylogenetic signal except for PBT and FBT and seem to evolve slower than expected by climate change, and 5) phylogenetic signal can be used to predict traits for other species, which can help the application of more trait data demanding methods for biodiversity assessment and forecast.

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SUPPORTING INFORMATION

Table S1
Table S2
Table S3
Table S4

Table S1. List of species, number of individuals, mean and variance of the variables used in this work.

Sp		FBT		Weight		SVL		PBT		CT$_{min}$		CT$_{max}$	
	N	Mean	Var	Mean	Var	Mean	Var	Mean	Var	Mean	Var	Mean	Var
L.belli	10	32.90	5.94	10.48	20.38	69.24	69.88	36.85	0.32	3.86	5.15	45.33	0.15
L.bisignatus	11	34.28	1.21	7.66	8.03	64.47	66.27	35.31	6.24	8.22	3.19	46.24	0.58
L.buergeri	10	34.62	3.75	16.73	50.32	78.28	124.53	36.61	1.09	8.73	7.05	45.51	0.25
L.carlosgarini	10	34.15	12.37	6.00	2.68	59.90	44.69	36.07	1.14	8.99	4.55	45.50	0.87
L.cf.monticola	1	-	-	12.90	-	82.70	-	37.33	-	8.20	-	45.60	-
L.chiliensis	9	34.55	0.13	11.93	6.41	74.29	38.98	35.66	1.11	7.96	1.97	45.05	0.39
L.confusus	13	-	-	3.73	1.46	49.99	29.25	36.90	1.55	7.67	4.71	45.74	0.29
L.constanzae	14	27.29	28.28	5.26	2.89	56.87	37.81	34.51	2.63	7.84	13.33	42.45	1.01
L.curis	3	33.50	10.53	22.27	16.86	87.36	30.93	35.66	3.02	7.80	10.53	45.10	0.09
L.curiscensis	13	34.81	3.30	4.17	1.97	49.71	153.48	36.65	1.27	5.45	5.50	45.73	0.27
L.escarchadosi	9	13.54	16.88	66.56	222.83	7.73	3.27	34.56	1.20	3.73	2.24	43.73	0.34
L.fitzgeraldi	15	25.64	14.24	3.15	1.95	47.67	45.01	34.72	1.37	6.95	9.03	45.34	0.32
L.flavipiceus	2	34.25	0.25	15.80	23.12	78.45	51.00	37.28	0.53	7.45	0.25	46.30	1.62
L.foxi	9	33.98	1.30	7.48	4.06	65.73	57.19	33.28	0.59	9.16	17.96	42.40	0.25
L.fuscus	6	33.26	6.78	2.63	1.27	44.93	77.48	36.28	0.39	8.36	1.02	44.92	0.09
L.isabellae	4	34.23	0.69	11.67	4.12	80.35	44.93	37.68	0.66	7.55	3.98	46.75	0.22
L.josephorum	6	33.76	3.09	3.81	1.59	51.42	39.04	36.09	0.38	7.94	4.79	45.82	0.15
L.lemniscatus	12	34.04	1.40	2.74	0.31	47.36	17.39	35.29	1.24	7.21	4.42	44.54	0.67
L.leopardinus	4	27.00	58.32	13.30	109.52	71.34	402.14	35.60	1.49	4.60	5.59	45.28	1.75
L.magellanicus	2	20.90	48.02	54.34	37.41	5.30	0.32	34.17	0.76	1.40	4.50	43.10	-
L.maldonadae	2	-	-	-	-	-	-	36.90	0.27	5.65	6.85	45.50	0.72
L.monticola	8	36.50	2.35	4.87	3.85	56.24	112.53	36.31	2.14	8.04	7.77	45.60	1.04
L.moradoensis	12	32.95	1.23	3.42	1.67	50.76	61.42	35.29	1.38	8.26	6.79	45.13	0.18
L.nigroviridis	14	31.00	40.11	10.77	9.28	69.82	48.56	35.24	6.85	6.50	12.03	45.49	0.26
L.nitidus	6	35.22	16.29	22.73	133.02	85.08	340.66	36.05	4.80	6.82	4.58	45.18	3.23
L.patriciaiturriae	4	34.80	-	16.28	29.05	88.49	90.55	34.63	10.02	4.40	4.94	45.38	0.49
L.paulinae	1	37.90	-	3.06	-	50.36	-	34.45	-	14.20	-	43.40	-
L.pictus	23	33.13	2.52	6.52	0.71	63.16	13.39	36.02	1.18	4.00	2.47	46.33	1.60
L.platei	10	33.31	1.69	3.40	1.44	48.67	20.02	36.25	1.93	8.99	5.24	44.85	1.79
L. pseudolemniscatus	4	35.60	2.48	1.31	0.09	36.39	1.39	34.27	5.19	-	-	47.00	3.92
L.rosenmanni	11	26.93	20.45	4.38	9.22	54.38	121.52	35.50	1.46	5.29	8.89	44.80	0.69
L.schmidti	10	27.59	2.12	3.63	2.65	49.74	43.30	34.59	2.79	8.99	9.70	43.95	2.84
L.schroederi	5	33.10	0.49	4.26	2.20	54.75	58.09	36.07	1.78	8.04	9.23	45.46	0.26
L.tenuis	13	33.77	0.37	4.49	0.86	53.77	20.67	37.04	1.26	9.08	1.59	45.04	1.28
L.valdesianus	1	31.30	-	25.20	-	87.84	-	-	-	-	-	-	-
L.velosoi	3	36.37	1.01	4.10	0.01	53.59	1.51	33.33	13.60	9.07	3.52	45.47	0.69
L.villarricensis	1	-	-	-	-	-	-	-	-	-	-	-	-
L.zapallarensis	18	35.09	3.13	9.28	19.06	62.51	224.57	34.36	6.81	8.43	4.50	45.22	0.86

Table S2. Pearson moment correlation matrix (non phylogenetically corrected) between traits and between traits and variables. Numbers written in bold in the lower-left half-matrix show correlations that are signifficant at the 95% confidence interval. Numbers written in bold in the upper-right half-matrix shows correlations that are signifficant at the 95% confidence interval corrected using a Bonferroni approach.

	FBT	PBT	CT_{min}	CT_{max}	Weight	SVL	MaxTa	MeanTa	MinTa	Prec
FBT	1	0.25927	0.576719	0.436416	0.081042	0.050824	0.537518	0.33639	0.261502	0.094892
PBT	0.25927	1	-0.046841	0.54599	0.249873	0.269136	0.092741	-0.161145	-0.076551	0.460763
CT_{min}	0.576719	-0.046841	1	-0.195778	-0.214813	-0.235205	0.510764	0.351647	0.127805	-0.19891
CT_{max}	0.436416	0.54599	-0.195778	1	0.186856	0.156419	0.110844	0.034524	0.177235	0.328026
Weight	0.081042	0.249873	-0.214813	0.186856	1	0.936526	-0.252528	-0.364869	-0.319945	0.179452
SVL	0.050824	0.269136	-0.235205	0.156419	0.936526	1	-0.288926	-0.344463	-0.283497	0.183207
MaxTa	0.537518	0.092741	0.510764	0.110844	-0.252528	-0.288926	1	0.828751	0.72791	0.031259
MeanTa	0.33639	-0.161145	0.351647	0.034524	-0.364869	-0.344463	0.828751	1	0.945033	-0.303048
MinTa	0.261502	-0.076551	0.127805	0.177235	-0.319945	-0.283497	0.72791	0.945033	1	-0.158619
Prec	0.094892	0.460763	-0.19891	0.328026	0.179452	0.183207	0.031259	-0.303048	-0.158619	1

Table S3. *P*-values for Pearson moment correlation matrix (non phylogenetically corrected) between traits and between traits and variables. Numbers written in bold in the lower-left half-matrix show correlations that are signifficant at the 95% confidence interval. Numbers written in bold in the upper-right half-matrix shows correlations that are significant at the 95% confidence interval corrected using a Bonferroni approach.

	FBT	PBT	CT_{min}	CT_{max}	Weight	SVL	MaxTa	MeanTa	MinTa	Prec
FBT	0	1	0.024757	0.500132	1	1	0.047001	1	1	1
PBT	0.145113	0	1	0.025745	0.147712	0.117956	1	1	1	0.184769
CT_{min}	0.00055	0.789319	0	1	0.215261	0.173789	0.06558	1	1	1
CT_{max}	0.011114	0.000572	0.252488	0	0.275179	0.362287	1	1	1	1
Weight	0.64866	1	1	1	0	0	1	1	1	1
SVL	0.775296	1	1	1	0	0	1	1	1	1
MaxTa	0.001044	0.585109	0.001457	0.513683	0.131579	0.082855	0	0	3.00E-006	1
MeanTa	0.051749	0.340686	0.035456	0.83925	0.026391	0.036821	0	0	0	1
MinTa	0.1352	0.65248	0.457591	0.293987	0.053552	0.089067	0	0	0	1
Prec	0.593465	0.004106	0.244826	0.047474	0.287892	0.277755	0.846164	0.054103	0.321911	0

Table S4 Bonferroni adjusted *P*-values for phylogenetically corrected correlations between traits and between traits and environmental variables.

	FBT	PBT	CT_{min}	CT_{max}	Weight	SVL
FBT						
PBT	1					
CT_{min}	0.1746634	1				
CT_{max}	1	0.300508	1			
Weight	7.638E-005	1	0.3007637	1		
SVL	0.06501159	1	1	1	1	
MaxTa	1	1	0.09752461	1	1	1
MeanTa	1	0.4866899	1	1	1	1
MinTa	1	1	1	1	1	1
Prec	1	1	1	1	1	1


S. Luis
Carapari
Oran
Morguital
Ft. Pizarro or Soria
Llanos
Mataguayos
Matacos
Esquino
Gran Chaco
El Gran Chaco
Mansos
R. Vermejo
Calaalet
S. Bernardo
Tobas
Macapillo
S. Mig.
Petacas
Labrea
Maravilla
Native Iron
Sanchacorra
Taria
Matara
Anataya
la Torre
R. Salado
Socoucho
Sabagasta
Cardoso
Abipones
L. Sa. de los Porongos
la Reyna
Arsinusa
Cululu
Tio
Sa. Fe
Ranchos
Bajada or Parana
P. Gorda
Coronda
Herradura
S. Espiritu
S. Carlos
Rosario
Esquina
F. India
Melinque
Nicolas
Pergamino
S. Pedro
Baradero
Mercedes
Rojas
Arrecifes
Zarate
Salto
F. Federacion
Mar Chiquita
Ramada
L. Gomez
Luxan
Navarro
S. Vicente
Buenos Ayres
Quilmes
Ensenada
Magdalena
Canuelas
Monte
Pt. Piedras
Samborombon
Samborombon B.
R. Salado
F. del 25 de Mayo
L. Cabeza del buey
F. Laguna Blanca
Ca. Zapata
Ca. Larga
L. del Monte
Dolores
C. S. Antonio
R. Tuyu
Tapalquen
Tandil
R. Grande
Mar Chiquita
Vulcan
C. Corrientes
Curamoala
Sa. Ventana
Ft. Argentino
Port Belgrano
Quequen
Buenos Ayres
Rio de la Plata
Monte Video
Maldonado
S. Carlos
Rocha
C. S. Maria
Castilhos Gdes.
Candelones
Minas
Colonia
Rosario
Banda Oriental del Uruguay
Pay Sandu
Mercedes
Durazno
Monzon
Porongos
C. Largo
Melo
Cerrito
Pueblo
R. Negro
Belen
Purificacion
R. Arapey
Salto
Corrientes
Entre Rios
Missiones
Yapeyu
Concepcion
S. Tome
S. Borja
Alegrete
Itaqui
Tecla
R. Uruguay
Rio Grande do Sul
S. Pedro
Rio Pardo
Porto Alegre
L. dos Patos
Rio Grande
L. Mangueira
R. Jaguarão
Taim
S. Miguel
Chuy
Corrientes
Caacaty
Itati
Goya
S. Roque
Curuzu cuatia
Senhor hallado
S. Fernando
R. Negro
Santo Tomé
Candelaria
Corpus
Ytapua
Villa Rica
Caazapa
Yaguaron
Ytá
Asuncion
Emboscada
Curuguaty
Ygatimi
Villa Real
Tobati
Ipané
R. Ibobi
R. Tepoti
R. Paraguay
R. Pilcomayo
R. Parana
R. Pardo
R. Paranapanema
Guayra
Ciudad Real del Salto
Salto de 7 Quedas
Tapiraz
N. S. de Pacanana
R. Iguazu
Salto Iguazu
R. Curitiba or Yguazu
R. Uruguay
Sn. Pedro
R. Ygurey
R. Amambay
Paraguay

Chapter IV

Capítulo IV

Operative temperature as a predictor of lizard species distributions

INTRODUCTION

It is widely held that climate exerts a strong influence on species range limits (Darwin 1856, Wallace 1876, MacArthur 1972) and temperature stands out as one of the key variables (Lieth and Whittaker 1975; Rohde 1992). The use of climate variables is quintessential to studies attempting to explain the current distributions of species (for a review see Elith and Leathwick 2009) and predict their altered distributions under past and future climate change (eg. Peterson et al. 2002, Thomas et al. 2004, Thuiller et al. 2005, Araújo and Guisan

2006, Hof et al. 2011, Devictor et al. 2012). However, atmospheric climatic conditions interpolated across the surface of the earth are but a surrogate of the complex biophysical processes controlling species range limits on the ground. With the aim to improve the mechanistic link between climate and species distributions, we use a biophysical approximation of the thermal environment by estimating the operative temperature (Te) of a theoretical ectotherm. We then use the operative temperature as a predictor variable in bioclimatic envelope models applied to Iberian lizards and compare the resulting projections with that of models fitted with air temperature.

The suggestion that bioclimatic envelope models should be fitted with direct (causal) variables has been made in several occasions (Austin 2007, Elith and Leathwick 2009, Kearney and Warren Porter 2009). Using direct, rather than indirect variables, should be particularly important when using models to predict the effects of climate change on species ranges (e.g.,Guisan and Zimmermann 2000). However, the choice of the variables is often driven by the availability of climate variables (e.g., www.worldclim.org). Exceptions include derived bioclimatic variables used for modelling vegetation dynamics, such as growing degree-days or moisture indices that more directly relate to plant physiological processes (e.g. Prentice et al. 1992, Sykes and Prentice 1996, Hannah et al. 2013). For animals, however, meaningful bioclimatic variables are rarely used.

In part, this is due to the difficulty of acquiring detailed knowledge of the links between atmospheric conditions and the physiological processes determining species distributional dynamics. Even when detailed ecophysiological knowledge exists for a given species, there usually are difficulties in translating such knowledge into bioclimatic variables that are relevant for animals. One example is the computation of operative temperature, defined as the ‘equilibrium temperature of a non-regulating ectotherm’ (Hertz et al. 1993). In contrast with air temperature, operative temperature characterizes the expected temperature of the body of an non-thermoregulating animal taking into account a variety of climatic variables (e.g., solar radiation, air temperature and wind speed) and the physical properties of the organism (e.g., body size, shape, colour). The mathematical computation of operative temperature requires detailed climatic information with extremely high temporal resolution (minutes to hours) that is typically unavailable for most ecologists (but see Kearney et al. 2012, 2014).

Climate change is believed to have a deep impact in the future of biodiversity, and it has already increased global temperatures by 0.7 ºC (IPCC 2013). With it, operative temperatures must have increased too. But has this increment already caused a noticeable effect in species habitats and niches? There are several examples of climate change during the last century already affecting species ranges (Hickling et al. 2005, 2006) and even local extinctions have been reported (Sinervo et al. 2010). Those studies relate changes in the distribution of species with changes in the distribution of temperatures (such as poleward shift of the isotherm) (Chen et al. 2011). The problem is that for most of the species, populations and geographical regions there is no temporal data available that allows the observation of range shifts or population changes. Here we take an indirect approach, by projecting a niche model to the different time periods and evaluate if the projected potential distributions show an increasing or decreasing trend.

In order to examine if operative temperature for a prototypical organism is a better predictor of the distribution of reptile species than air temperature, we compared species distributions models fitted with mean operative temperature across 1956-2010 with equivalent models fitted with mean air temperature for the same period. Models fitted with operative temperature and air temperature are then projected into 5 year time slices spanning the period of 1956 and 2010 to examine if the use of a biophysical variable shows different temporal trends for the potential distribution of species.

MATERIALS AND METHODS

CLIMATE MODEL

Biophysical approaches to estimate operative temperatures (e.g., Buckley 2008) or steady state/transient organismal temperatures (e.g., Porter et al. 1973) require climatic data at a vey high temporal resolution. However, available climate databases for ecologists usually consist on climate averages across coarse resolution time slices (e.g. monthly averages). To address this problem, ecologists have used interpolation techniques to estimate hourly or sub-hourly profiles from these global averages. Maximum and minimum air temperatures are usually interpolated applying sinusoidal functions between minimum and maximum values that are assigned at specified daily hours (e.g., Buckley 2008) to create hourly (or fraction of an hour) profiles. Such interpolations cannot, however, account for the intra-day variation in weather conditions and makes it difficult to incorporate local climate variations such as morning mists or afternoon storms common in local areas that modify daily profiles.

In our study, instead of using climatic averages, we used the output of a regional climate simulation for the Iberian Peninsula. The variables were extracted at 1-hour temporal resolution from 1956 to 2010 using Advanced Weather Research and Forecasting model (WRF-ARW). The regional climate simulation was performed using the WRF-ARW model and designed at a horizontal resolution of 5 km (Prasad Dasari et al. 2014). The model is designed with three nested domains of 75, 25 and 5 km. The 5 km domain is located over the Iberian Peninsula region. The model performance for Iberian Peninsula region and its design are presented in Prasad Dasari et al. 2014 and in Appendix 2.

The initial boundary conditions were derived from NCEP 2.5 degree latitude / longitude resolution global analysis fields (Kalnay et al. 1996). The outputs of the model were extracted at 1 hour temporal resolution for the whole period. The output variables were sliced in 5 year periods, and averages were created using the library CDO (Mueller & Schulzweida 2013). In addition an averaged yearly profile was created for the variables used to calculate operative temperature for every 5 year period. For that, every value was averaged with the other values belonging to the same hour and day but of a different years. This way we created yearly profiles at 1 hour resolution for each time bin. Those yearly profiles were used to calculate operative temperatures and the mean was calculated for every 5 year period. The mean of all the time bins was also calculated. Air temperatures were also averaged in a similar fashion.

OPERATIVE TEMPERATURE

Operative temperature was calculated using the approach from Porter et al. 1973, solving a steady-state energy balance equation including solar shortwave radiation, thermal radiation and convection. We did not include evaporative cooling, metabolic heat production and conduction as they were estimated neglegible by Porter et al. 1973. The heat-flow (Q_e) is defined by Equation 1 in which Q_{is} is the shortwave solar radiation absorbed by the organism, Q_{ir} is the longwave (thermal) radiation absorbed by the animal, Q_{oi} is the thermal radiation emitted by the organism and Q_{conv} is the heat interchanged by convection.

$$Q_e = Q_{is} + Q_{ir} - Q_{oi} - Q_{conv}$$

Equation 1. Thermal energy balance. Where Q_{is} is estimated as in Equation 2, Q_{ir} is estimated as in Equation 4, Q_{oi} is estimated as in Equation 5, and Q_{conv} Is calculated as in Equation 6.

$$Q_{is} = \alpha \cdot (S_d \cdot SA \cdot F + Q_{sol} \cdot SA_{norm} + RAD_r \cdot SA \cdot F)$$

Equation 2. Shortwave radiation absorbed by the organism. Where α is the absorbance to shortwave solar radiation (0.85), S_d represents the shortwave diffuse radiation reaching the animal surface (see Table 1), *SA* represents the total surface area (see Table 1), *F* is the view factor for direct radiation (see Table 1), Q_{sol} is the total shortwave solar radiation reaching ground, SA_{norm} is surface area normal to sun (see Table 1) and RAD_r represents the upward (reflected) solar radiation reaching the organism (Table 2). Q_{sol} is calculated as in Equation 3.

$$Q_{sol} = (RAD / \cos(ZEN))$$

Equation 3. Shortwave solar radiation normal to ground. Where *RAD* is the direct downward shortwave radiation from the sun (Table 2) and *ZEN* is the solar zenith angle in radians.

$$Q_{ir} = SA \cdot F \cdot \sigma \cdot \varepsilon \cdot RAD_i + SA \cdot F \cdot \sigma \cdot \varepsilon \cdot RAD_{ir}$$

Equation 4. Infrared radiation absorbed by the organism. Where σ is the Stephan-Boltzman constant (5.670373e-8 W/m^2/k^4), ε is the emissivity of the animal (0.95), RAD_i is the incoming thermal radiation and RAD_{ir} is the incoming reflected thermal radiation (see Table 2).

$$Q_{oi} = SA \cdot \sigma \cdot \varepsilon \cdot (T_e)^4$$

Equation 5. Thermal radiation emitted by the organism. Where T_e is the operative temperature.

$$Q_{\text{conv}} = SA \cdot 3.49 \cdot (ws/L)^{0.5} \cdot (T_{\text{e}} - T_{\text{air}})$$

Equation 6. Heat interchanged by convection. Where *WS* is windspeed in m/s, *L* is the characteristic dimension of the animal (see Table 1), and T_{air} is air temperature at 2m. As T_{e} is required to estimate Q_{conv} and Q_{oi} an iterative procedure is needed to find a steady-state solution for the equation.

Table 1. : Parameters used in the operative temperature model.

Alias	Value	Units and explanation
α	0.85	Skin absorbance to shortwave radiation
S_{d}	*RAD*/10	Shortwave diffuse radiation reaching the animal
mass	10 g	Body mass
L	$(\text{mass}*10^{-6})$ ^ (1/3)	Characteristic dimension (Mitchel 1976)
SA	$(10.4731*\text{mass}^{0.600})/10000\ \text{m}^2$	Total surface area. M. Kearney pers. com.
SA_{norm}	$(3.798*\text{mass}^{0.683})/10000\ \text{m}^2$	Surface area normal to sun. M. Kearney pers. com.
F	0.6	View Factor (Porter 1973)
ZEN	0.2	Rad. Zenith angle of the sun
σ	5.670373e-8 $\text{W/m}^2/\text{k}^4$	Stephan-Boltzman constant

Table 2. RCM output variables used for the calculation of operative temperatures.

Alias	WRF-ARW model variable	Use in our model
WS	u 10 0 x-wind component (m s-1) at 10 m height	Used to calculate ws
	v 10 0 y-wind component (m s-1) at 10 m height	Used to calculate ws
T_{air}	t2 1 0 TEMP at 2 M (K)	Air temperature at 2 m
RAD_{i}	lwdnb 1 0 INSTANTANEOUS DOWNWELLING LONGWAVE FLUX AT BOTTOM (W m-2)	Longwave radiation reaching the surface
RAD_r	swupb 1 0 INSTANTANEOUS UPWELLING SHORTWAVE FLUX AT BOTTOM (W m-2)	Reflected shortwave radiation
RAD	swdnb 1 0 INSTANTANEOUS DOWNWELLING SHORTWAVE FLUX AT BOTTOM (W m-2)	Shortwave radiation reaching the surface
RAD_{ir}	lwupb 1 0 INSTANTANEOUS UPWELLING LONGWAVE FLUX AT BOTTOM (W m-2)	Longwave radiation coming from the earth surface

SPECIES DISTRIBUTIONS DATA

The study was developed across the Iberian Peninsula. Species distributions data are taken from Araújo et al. 2011. The dataset consists of a compilation of reptile species data for Portugal and Spain at 10km resolution. For Spain, the original information was from the "Inventario Nacional de Biodiversidad de España" by the "Dirección General de Medio Natural y Política Forestal" (Ministerio de Agricultura, Alimentación y Medio Ambiente, n.d.). For Portugal, the species distributions information was compiled from a variety of different sources (see references provided in Araújo et al. 2011).

SELECTED SPECIES

We restricted analysis to lacertid lizard species from mainland Iberian Peninsula. Other groups of reptiles (e.g., turles, skinks or snakes) differ in body shape, and geckos—being mainly nocturnal— cannot be treated as heliotherms (i.e., organisms that use radiation to regulate body temperature). From those candidate species we only selected those who appeared in least ten 10 X 10 km grid cells to assure that the number of variables will not be higher than one tenth the number of records (Harrell et al. 1996). 14 species met this criteria (Table S1).

BOCLIMATIC MODELLING OF SPECIES DISTRIBUTIONS

We used Generalized Linear Models with a logistic transformation (McCullagh & Nelder 1989) to create the bioclimatic envelope models. Each species dataset was randomly divided into calibration and validation subset of 75% and 25% of the species ranges respectively; the procedure was repeated 50 times maintaining the species prevalence constant. Models were fitted either with mean annual operative temperature or mean annual atmospheric temperature between 1956 and 2010 as a single predictor variable. Threshold for model presence-absence was estimated as the threshold to maintain the observed prevalence.

Models fitted with operative temperature and air temperature were projected into the mean air and operative temperatures of each 5 year time slices from 1956 to 2010 and the potential distributional range area for every species was calculated for each projection. Linear regression was fitted to the temporal sequence of species potential distributions to show the temporal trend of projected ranges for each species. To test if the magnitude of temporal trends differ significantly between air temperature ensembles and operative temperature ensembles we used Wilcoxon rank sum test on the absolute slopes of regression lines of air temperature projections and operative temperature projections.

RESULTS

AIR TEMPERATURE AND OPERATIVE TEMPERATURE MODELS

Univariate models fitted with air temperature and with operative temperature did not show strong differences in their predictions (Table 3, Figure 1). Summary statistics show that for most species models discriminated poorly, although variably. Overall, models performed better for species associated to mountain areas or with a globally European or Euro-siberian distribution than for more typically Mediterranean species.

True Skill statistic averaged 0.14 for air temperature models, and 0.1 operative temperature models, kappa averaged 0.13 for air temperature and 0.1 for operative temperature models, average accuracy was 0.7 for air temperature and 0.68 for operative temperature models, specificity and sensitivity were 0.83 and 0.3 for air temperature respectively and 0.83 and 0.27 for operative temperature respectively, finally, average AUC was 0.7 for air temperature and 0.68 for operative temperature.

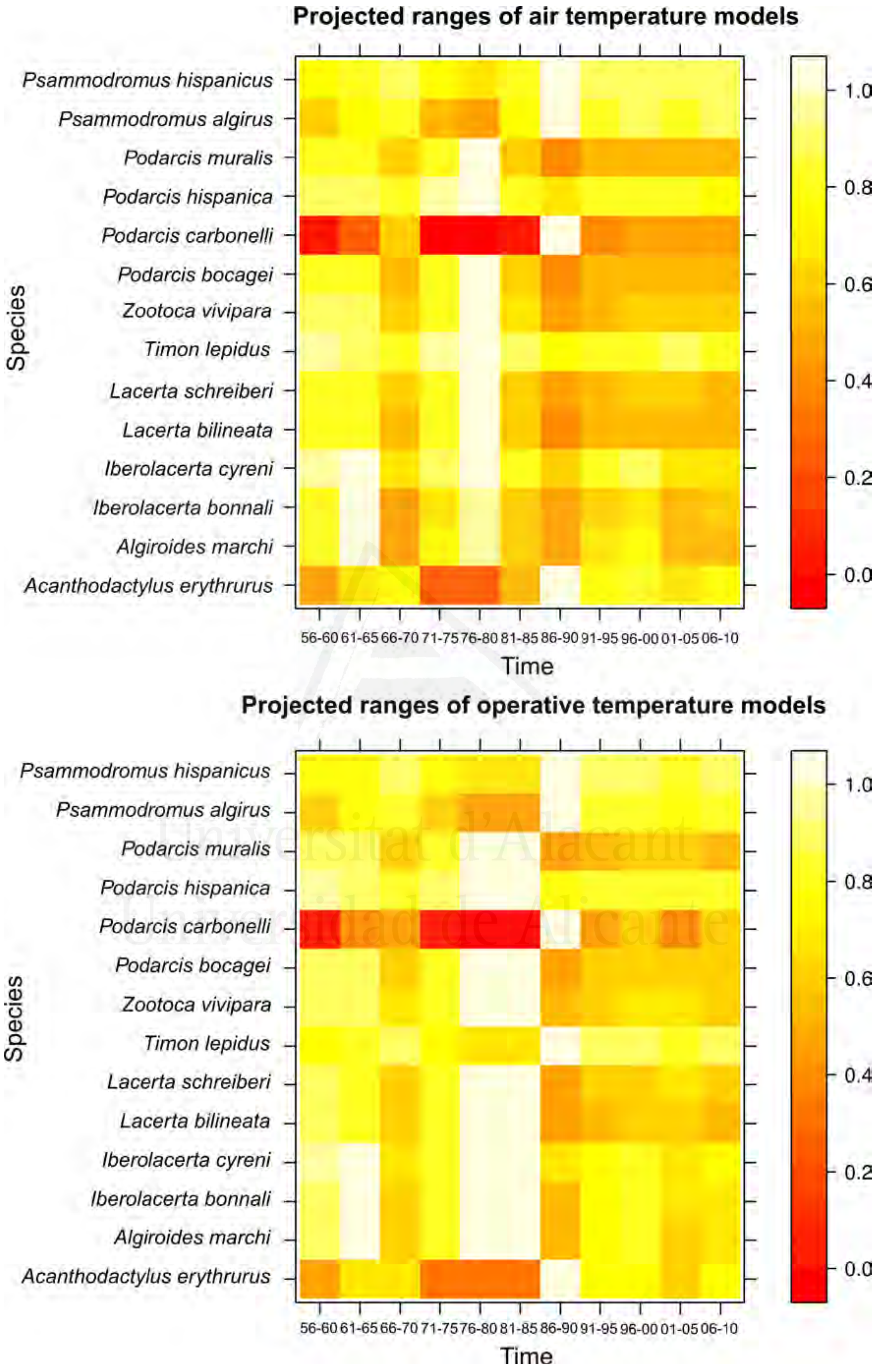

Figure 1. Relative change in projected range (0 to 1) for the studied species for models fitted with air temperature (above) and operative temperature (below).

Table 3. Summary statistics of Generalized Linear models for air temperature and operative temperature.

	TSS	Kappa	Accuracy	Specificity	Sensitivity	AUC
Air Temperature						
Acanthodactylus erythrurus	0.06156	0.06156	0.62756	0.8803	0.1812	0.62756
Algiroides marchi	-0.004	-0.004	0.70154	0.996	0	0.70154
Iberolacerta bonnali	0.65712	0.62258	0.99824	0.99804	0.65892	0.99824
Iberolacerta cyreni	-0.006	-0.006	0.89192	0.994	0	0.89192
Lacerta bilineata	0.20738	0.2068	0.8124	0.94816	0.2594	0.8124
Lacerta schreiberi	0.06416	0.06402	0.60788	0.86938	0.19472	0.60788
Timon lepidus	0.00284	0.00284	0.50052	0.37236	0.63046	0.50052
Zootoca vivipara	0.23522	0.23354	0.83406	0.97596	0.25944	0.83406
Podarcis carbonelli	-0.011	-0.011	0.58474	0.989	0	0.58474
Podarcis bocagei	0.04082	0.04082	0.62116	0.93924	0.1016	0.62116
Podarcis hispanica	0.07596	0.07596	0.56638	0.45532	0.62066	0.56638
Podarcis muralis	0.34516	0.34486	0.83482	0.93818	0.40708	0.83482
Psammodromus algirus	0.05024	0.0502	0.57164	0.78214	0.26808	0.57164
Psammodromus hispanicus	0.17566	0.17572	0.61592	0.53404	0.64188	0.61592
Operative temperature						
Acanthodactylus erythrurus	0.03588	0.03588	0.60954	0.8772	0.1586	0.60954
Algiroides marchi	-0.004	-0.004	0.56444	0.996	0	0.56444
Iberolacerta bonnali	0.3547	0.3363	0.99246	0.99698	0.35768	0.99246
Iberolacerta cyreni	-0.006	-0.006	0.83306	0.994	0	0.83306
Lacerta bilineata	0.20608	0.20546	0.80734	0.948	0.25808	0.80734
Lacerta schreiberi	0.02916	0.02916	0.61076	0.86562	0.16368	0.61076
Timon lepidus	-0.00194	-0.00194	0.50436	0.36836	0.6297	0.50436
Zootoca vivipara	0.19212	0.19086	0.81298	0.97456	0.21734	0.81298
Podarcis carbonelli	-0.011	-0.011	0.62472	0.989	0	0.62472
Podarcis bocagei	0.03378	0.03366	0.65548	0.93936	0.09446	0.65548
Podarcis hispanica	0.04946	0.04946	0.55652	0.43948	0.60996	0.55652
Podarcis muralis	0.30094	0.30062	0.81958	0.9339	0.36694	0.81958
Psammodromus algirus	0.04946	0.04936	0.57594	0.78188	0.26752	0.57594
Psammodromus hispanicus	0.16886	0.16886	0.6127	0.53012	0.63892	0.6127

RANGE PROJECTIONS ACROSS TIME FOR AIR TEMPERATURE AND OPERATIVE TEMPERATURE MODELS

Potential ranges from air temperature model projections changed slightly more steeply than potential ranges from operative temperature model projections (Figure 1, Table 4). The slopes of ten out of the fourteen species for air temperature and nine out of ten for operative temperature models was negative (their potential range is reducing with time), only for *Timon lepidus* model projections the trend show a different sign for air temperature and for operative temperature. Nevertheless, the slope *P*-values are either not significant or marginally significant at the level of 0.05 (Table 4). Finally, the paired Wilcoxon Rank

Table 4. Estimates, standard error and *P*-values of temporal trends of projected lizard ranges.

	Intercept	Slope	Intercept SE	Slope SE	Intercept *P*-val	Slope *P*-val
Air Temperature						
Acanthodactylus erythrurus	599.5091	35.7636	182.1137	26.8512	0.0093	0.2156
Algiroides marchi	37.8727	-1.2364	4.8035	0.7082	2.4859E-005	0.1148
Iberolacerta bonnali	38.9273	-1.2909	4.9075	0.7236	2.3692E-005	0.1081
Iberolacerta cyreni	51.5273	-1.2091	4.6200	0.6812	1.4327E-006	0.1096
Lacerta bilineata	570.2182	-22.9000	64.1666	9.4608	9.4708E-006	0.0386
Lacerta schreiberi	1109.2182	-39.9455	119.1204	17.5633	6.4569E-006	0.0490
Timon lepidus	4487.3818	-42.6545	184.2064	27.1598	1.5846E-009	0.1507
Zootoca vivipara	257.3091	-9.1273	26.6985	3.9365	4.8611E-006	0.0456
Podarcis carbonelli	546.0364	-21.3091	61.0718	9.0046	9.0107E-006	0.0422
Podarcis bocagei	30.1091	10.2545	51.2995	7.5637	0.5717	0.2082
Podarcis hispanica	3932.9818	-57.3455	196.7896	29.0150	9.1369E-009	0.0795
Podarcis muralis	813.8000	-32.8909	89.0406	13.1283	7.5263E-006	0.0336
Psammodromus algirus	1175.4545	43.2273	167.6598	24.7201	6.2488E-005	0.1143
Psammodromus hispanicus	3073.1273	66.4636	216.4039	31.9070	1.8132E-007	0.0669
Operative temperature						
Acanthodactylus erythrurus	535.4727	32.5727	171.5986	25.3008	0.0123	0.2301
Algiroides marchi	43.1455	-1.1000	4.6414	0.6843	6.5481E-006	0.1424
Iberolacerta bonnali	43.8727	-1.0545	4.7735	0.7038	7.1887E-006	0.1683
Iberolacerta cyreni	57.7273	-1.3182	4.6856	0.6908	6.1507E-007	0.0887
Lacerta bilineata	585.9273	-20.4273	66.8644	9.8586	1.0616E-005	0.0681
Lacerta schreiberi	1162.0727	-37.3000	130.7816	19.2827	9.4789E-006	0.0851
Timon lepidus	3359.4364	63.5636	260.3392	38.3849	4.1378E-007	0.1321
Zootoca vivipara	259.3818	-8.3364	26.7117	3.9384	4.5673E-006	0.0634
Podarcis carbonelli	566.9273	-19.9727	63.0630	9.2981	8.6172E-006	0.0602
Podarcis bocagei	15.8000	8.8818	37.2079	5.4860	0.6811	0.1399
Podarcis hispanica	4015.5818	-52.1727	218.3006	32.1867	1.9E-008	0.1395
Podarcis muralis	830.5455	-29.6818	98.7822	14.5646	1.4846E-005	0.0720
Psammodromus algirus	1118.9273	36.3455	181.7533	26.7981	1.6744E-004	0.2081
Psammodromus hispanicus	2981.2909	63.9818	247.3228	36.4658	7.41E-007	0.1132

Sum Test between the slopes of air temperature projections and operative temperature projections failed to reject the null hypothesis ($V = 70$, $P = 0.094$).

DISCUSSION

Our results do not support our prediction that a variable closely linked to physiological processes controlling species local performance and distribution (operative temperature) should discriminate species potential distributions better than a variable less directly linked to such processes (air temperature). In fact, models projected between 1956 and 2010 seem to estimate similar range changes if fitted with operative temperature instead of air temperature.

Even though comparisons between biophysical and bioclimatic envelope models are scarce, existing studies generally failed to find support for improved discrimination ability of mechanistically oriented models compared with the purely correlative. For example, Buckley et al. 2010 compared a number of biophysical and bioclimatic envelope models, and concluded that the discrimination ability of biophysical models was not higher than that of bioclimatic envelope models. Kearney et al. 2010 examined the congruence of Niche Mapper and Maxent projections and found results to be qualitatively similar, even though comparable measures of accuracy or goodness of fit were not provided between approaches. Our approximation is somehow different, as we do not construct a fully-fledged biophysical model, but our results, like those of Buckley et al. 2010 and Morin and Thuiller 2009 point out that a biophysical approach does not necessarily result in higher accuracy.

But if operative temperature is directly linked to the thermal physiology of reptile species, why does it not outperform models fitted with air temperature? One possibility is that operative temperature is more meaningful at smaller scales of resolution, being mainly a component to be expressed at the scale of the microenvironment (Hertz et al. 1993). The matter of scale is a recurrent issue in species distribution modeling (e.g., Guisan and Thuiller 2005, Araújo and Guisan 2006 and others), and has not yet been settled. The influence of a variable on the presence or absence of a species might be strong at a certain geographical scale while being less important at other scales (e.g., Pearson and Dawson 2003, Araújo and Rozenfeld 2014). Although operative temperature has been previously used to model niches at coarse scales of resolution and extent (e.g., Kearney et al. 2010, Buckley et al. 2011), it is a biophysical variable that is prone to great spatial heterogeneity due to small-scale variations in orography, land-cover and shadowing effects from microhabitat features (Sears et al. 2011). In practice, this means that within cell variation of operative temperature is bound to be extremely large and poorly representative by mean values. Although micro-climatic variation in air temperatures also exist (Scheffers et al. 2014), it probably is less variable than operative temperature.

Another explanation for the observed pattern is that most of the records for the studied species come from places and times where the air temperature is closer to the preferred temperature of the animal (i.e. the one that the lizards selects along a thermal gradient in the lab). Lizards can behaviouraly thermoregulate (Cowles and Bogert 1944) and thus decouple their internal temperature from that experienced in their direct environment (e.g. Marquet et al. 1989). The extent of thermoregulation may vary seasonally and affect the species activity pattern. As has been shown by Van Damme et al. 1987 *Zootoca vivipara* (one of our studied species) is less active above ground and deviates more from thermal conformity (i.e. the field temperature of the animal deviates more from the air temperature) during the cooler months and the opposite is true during the warmer months when air temperature is closer to the preferred one. If this is the case, and considering that this species hibernates and that adults emerge earlier and retreat later in mid-summer then it is likely that most records of this species will be summer ones. Further, since preferred temperature varies across subpopulations (Van Damme et al. 1986) it is likely that most records may come from areas where the lizards field temperature (the measured temperature of individuals in the field) is more closely correlated to the air temperature.

Another issue is error propagation. Variables have a certain degree of error, which propagates to the resulting outcome when combining them (Heuvelink et al. 1989). Error propagation has rarely been taken into account in species modelling studies. Operative temperature requires several input variables with varying degrees of uncertainty, making error propagation potentially more important than with air temperature. Biophysical models are usually trained with species-specific information. Radiative and convective properties vary depending on shape, size and color, which have an influence in operative temperature (Campbell and Norman 1998). In this article, we used a single lizard model to represent the operative temperature of 14 species of lacertid lizards morphologically similar but not identical.

When examining temporal projections of the model fitted with operative temperature and air temperature other issues emerge. Buckley et al. 2010 compared two correlative models (maxent and GLM) against three biophysical models and found that biophysical models predicted larger range shifts under climate change than correlative models. Kearney et al. 2010 on the other hand found that a correlative and an energy balance mechanistic approach projected similar changes in suitability under climate change conditions. However, this study modeled a nocturnal mammal rather than diurnal ectotherms. During the night, the contribution of radiation to operative temperature is practically null, so nocturnal operative temperatures approach air temperature. Also (Morin and Thuiller 2009) compared the projections of niche and process-based models for temperate trees under climate change. In this study, the process based model tended to predict lower proportion of extinction than the niche models.

The projected potential range sizes show weak trends that are positive for most of the tipically Mediterranean species (such as *Acanthodactylus erythrurus*, *Psammodromus algirus* and *Psammodromus hispánicus*) and *Podarcis carbonelli*, while they are negative for the species whose distribution expands to central Europe (such as *Lacerta bilineata*, *Zootoca vivipara*, *Podarcis muralis*) (Sillero et al. 2014), from high mountainous areas (such as *Iberolacerta* species) or associated to atlantic climates and humid areas (such as *Lacerta schreiberi*). *Algiroides marchi* shows a decreasing trend, although it is a Mediterranean species and does not live at high altitudes it is associated to a mountainous area in south east Spain (Pleguezuelos et al. 2002) with cooler environmental temperatures. Nevertheless, the trends detected are weak, and for many of the species the *P*-value of the slope is far from significant with TSS very close to 0.

Recent climate change has already caused a noticeable effect in several taxa (e.g., Parmesan et al. 1999, Hickling et al. 2005, Both et al. 2006, Parmesan 2006). Those effects have been detected when long-term monitorization has allowed to build a time series that allows the detection of such distributional changes. Nevertheless, even in developed countries most species have not been monitored in such a way so recent distributional or population changes can not be known. There is, nevertheless, a long time record from weather stations that allowed high resolution (both temporal and spatial) climate reconstructions (eg. Dasari et al. 2014b). This allowed us to compare current distributions with past and current states of the climate. In the case of Iberian reptiles, atlas data has a long time range spanning all 20th century (Pleguezuelos et al. 2002), and the date of the records is not yet readily available (Carretero pers. com.). Projecting the models to sequential time bins allows to estimate how their potential distribution is moving. The resulting trends are weak (Table 4) but consistent with evaluations of the potential effect of future climate change (Araújo et al. 2011).

This results hint on how climate change has been affecting lacertid lizards in Iberian Peninsula. For other taxa, this has resulted in a noticeable change in the distribution (Parmesan et al. 1999) and or phenology and abundance (eg. Visser and Both 2005, Both et al. 2006), nevertheless, herptiles are not expected to be good dispersers and amphibians can show a time lag of centuries following climate (Araújo and Pearson 2005), moreover in the Iberian Peninsula even farmland birds show a time lag of several decades in the response to changes in landscape and climate (Torres 2016). Is therefore very likely that current changes in potential habitat has not yet been translated in a distributional change of herpetofaunal species. With our data, species distributions models were able to fit the data similarly with air temperature and operative temperature. Given that information required for parameterization operative temperature is costly, further empirical evidence is required in support for its use as a bioclimatic variable in species distributions models. Although the mechanistic links between species physiology and operative temperature exists, its use as a variable in correlative models may not improve their predictive power.

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SUPPORTING INFORMATION

Figure S1
Figure S2
Table S1

Table S1. Species range size (in number of 10 X 10 km cells) in the Iberian Peninsula and average Snout-vent lengths (mm).

Sp	Range 10x10km	SVL	Source
Acanthodactylus erythrurus	779	80	Vertebrados Ibericos
Algiroides marchi	25	46	(Palacios et al., 1974; Eikhorst et al., 1979)
Iberolacerta bonnali	24	53.6	Arribas, 1994
Iberolacerta cyreni	35	87.5	Vertebrados Ibericos
Lacerta bilineata	398	108.7	Vertebrados Ibericos
Timon lepidus	3853	242	Vertebrados Ibericos
Lacerta schreiberi	849	98.2	Vertebrados Ibericos
Zootoca vivipara	190	49.7	Arribas 2009
Podarcis bocagei	387	56	Vertebrados Ibericos
Podarcis carbonelli	69	50	Vertebrados Ibericos
Podarcis hispanica	3606	60.1	Personal data
Podarcis muralis	577	58.5	Vertebrados Ibericos
Psammodromus algirus	3458	92	Vertebrados Ibericos
Psammodromus hispanicus	1400	51	(López y Martín, 2009)

Figure S2. Multi temporal ranges projections of T_{air} ensembles. The numbers in the yellow cells represent the five year period between 1956 and 2010 of the map below. Each row shows the maps for one species in the following order from top to bottom: 1.-*Acanthodactylus erythrurus*, 2.-*Algiroides marchi*, 3.-*Iberolacerta bonnali*, 4.-*Iberolacerta cyreni*, 5.-*Lacerta bilineata*, 6.-*Lacerta schreiberi*, 7.-*Lacerta lepida*, 8.-*Lacerta vivipara*, 9.-*Podarcis carbonelli*, 10.-*Podarcis bocagei*, 11.-*Podarcis hispanica*, 12.-*Podarcis muralis*, 13.-*Psammodromus algirus*, 14.-*Psammodromus hispanicus*.

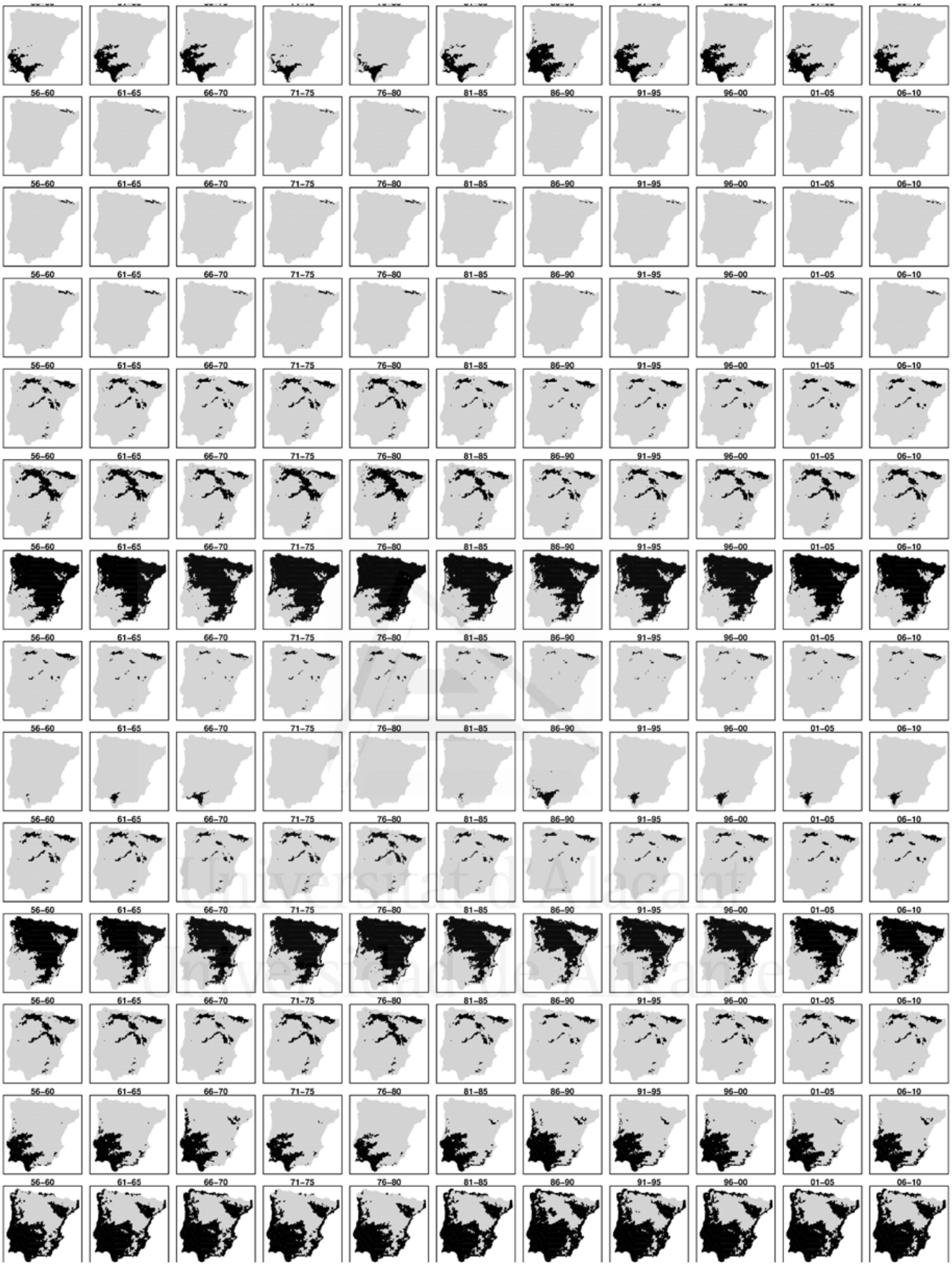

Figure S1. Multi temporal ranges projections of T_e ensembles. The numbers in the yellow cells represent the five year period between 1956 and 2010 of the map below. Each row shows the maps for one species in the following order from top to bottom: 1.-*Acanthodactylus erythrurus*, 2.-*Algiroides marchi*, 3.-*Iberolacerta bonnali*, 4.-*Iberolacerta cyreni*, 5.-*Lacerta bilineata*, 6.-*Lacerta schreiberi*, 7.-*Lacerta lepida*, 8.-*Lacerta vivipara*, 9.-*Podarcis carbonelli*, 10.-*Podarcis bocagei*, 11.-*Podarcis hispanica*, 12.-*Podarcis muralis*, 13.-*Psammodromus algirus*, 14.-*Psammodromus hispanicus*.

Conclusions

Conclusiones

CONCLUSIONS

1 Both thermal preferences, field temperatures and thermal limits show signs of conservatism (seem to have changed slower than expected by brownian motion alone).

2 Heat tolerance is largely conserved across terrestrial ectotherms, endotherms and plants. In contrast, tolerance to cold varies markedly between and within species.

3 To match the current rate of temperature increase, *Liolaemus* would have to evolve around 100.000 times faster than the normal evolutionary rate of those traits. This rate is in agreement with the rate previously estimated for realized niches.

4 Thermal preferences and field temperatures, as well as morphological characters show more phylogenetic signal than critical temperatures in *Liolaemus*.

5 The split between *Liolaemus* s.s. and *Eulaemus*, which sets the origin of diversification of the group is set at 27 mya, further back than previous estimations and questioning the hypothesis of Andean vicariance as the origen of diversification for *Liolaemus*.

6 Although vicariance by Andean uplift was probably not responsible for the *Liolaemus-Eulaemus* split, it probably was for the separation of the Argentinian members of *Liolaemus* s.s.

7 The spectral density analysis suggests a late diversification since the *Liolaemus-Phymaturus* split, so if ecological opportunity is the main driver of the radiation of *Liolaemus*, the opening of new niches was gradual.

8 Diversification rate was gradual and constant since the *Liolaemus-Eulaemus* split.

9 *Liolaemus* s.s. shows signs of an earlier type of diversification while *Eulaemus* seems to diversify faster towards more recent times.

10 Phylogenetic relatedness can mask the relationships between variables which is then revealed when the effect of phylogeny is removed. Adding to the importance of accounting for phylogenetic non-independence in comparative analyses.

11 Phylogenetic signal can be used to predict traits for other species, which can help the application of more trait data demanding methods for biodiversity assessment and forecast.

12 Using a direct variable does not necessarily increase the accuracy of correlative models.

13 Mediterranean species showed a weak positive trend in potential range and Atlantic, Alpine and central European species showed a weak negative trend during the period 1956-2010.

CONCLUSIONES

1 Las preferencias térmicas, la temperatura medida en campo y los límites térmicos muestran señales de conservatismo (parecen haber cambiado más despacio de lo que sería esperable exclusivamente por movimiento Browniano)

2 La tolerancia al calor está conservada en la mayor parte de los ectotermos, endotermos y plantas terrestres. En cambio, la tolerancia al frío varía de forma notable entre y dentro de las especies.

3 Para compensar la tasa actual de incremento de temperatura, los *Liolaemus* tendrían que evolucionar unas 100.000 veces más rápido de lo que estos rasgos evolucionan de forma normal. Esta tasa coincide con tasas estimadas anteriormente para nichos realizados.

4 Las preferencias térmicas y la temperatura en campo, así como los caracteres morfológicos muestran más señal filogenética que los críticos térmicos en *Liolaemus*.

5 Estimamos que la división entre *Liolaemus* s.s. y *Eulaemus*, que supone el origen de la diversificación del grupo, tuvo lugar hace 27 millones de años, más atrás que estimaciones anteriores y cuestionando la hipótesis de la vicarianza andina y el origen de la diversificación en *Liolaemus*.

6 Aunque la vicarianza por la elevación de los Andes no parece ser responsable de la división entre *Liolaemus* s.s. y *Eulaemus*, es probable que sí lo fuera de la separación de los miembros argentinos de *Liolaemus* s.s.

7 Los análisis de densidad espectral sugieren una diversificación tardía desde la división entre *Liolaemus* y *Phymaturus*, así que sí la oportunidad ecológica es el principal motor de la radiación de *Liolaemus*, la aparición de nichos nuevos fue gradual.

8 La tasa de diversificación a partir de la división entre *Liolaemus* y *Eulaemus* fue gradual and constante.

9 *Liolaemus* s.s. muestra señales de diversificación temprana, mientras que *Eulaemus* parece haberse diversificado más rápido hacia la actualidad.

10 El parentesco filogenético puede enmascarar las relaciones entre variables, las cuales pueden revelarse tras eliminar el efecto de la filogenia. Esto añade importancia al uso de análisis comparativos para compensar la no-independencia causada por la filogenia.

11 Se puede utilizar la señal filogenética para predecir el valor de los caracteres de otras especies, lo que puede ayudar a aplicar métodos que requieren mayor cantidad de datos para evaluar y predecir el estado de la biodiversidad.

12 Emplear variables directas no mejoran necesariamente la predicción de los modelos correlativos.

13 Las especies mediterráneas muestran una débil tendencia positiva en rango potencial durante el periodo 1956-2010, mientras que las especies atlánticas, alpinas y centroeuropeas muestran una débil tendencia negativa.

Appendices

Apéndices

ORIGINAL PUBLICATIONS

This PhD thesis has motivated the publication of seven original research articles in international forums by the date of this thesis deposit, in which I have significantly contributed in conceiving the idea, designing the study, collecting and analyzing data, discussing results and writing the manuscripts. The list of original publications is presented below and a copy of each article is available in the following pages.

ARTÍCULOS PUBLICADOS

Esta tesis ha dado lugar a la publicación de 7 trabajos de investigación en foros internacionales en el momento de depósito de la tesis, a los que he contribuido de forma significativa, concibiendo la idea, diseñando el estudio, tomando y analizando los datos, discutiendo los resultados y escribiendo los manuscritos. A continuación se presenta el listado de trabajos publicados y una copia de cada uno de ellos.

Apéndice 1.- Ferri-Yáñez, F., Hayes, J.P., Araújo, M.B. (2010). Hot research on roasted lizards: warming, evolution and extinction in climate change studies. Frontiers of Biogeography.

Apéndice 2.- Prasad Dasari, H., Pozo, I., Ferri-Yáñez, F., Araújo, M.B. (2014) A Regional Climate Study of Heat Waves over the Iberian Peninsula. Atmospheric and Climate Sciences.

Apéndice 3.- Araújo*, M.B., Ferri-Yáñez*, F., Bozinovic, F., Marquet, P.A., Valladares, F., Chown, S.L. (2013) Heat freezes niche evolution. Ecology Letters. (*These authors contributed equally to this study / Estos autores contribuyeron de forma similar al trabajo).

Apéndice 4.- Bozinovic, F., Ferri-Yáñez, F., Naya, H., Araújo, M.B., Naya, D.E. (2014) Thermal tolerances in rodents: species that evolved in cold climates exhibit a wider thermoneutral zone. Evolutionary Ecology Research.

Apéndice 5.- Garin, C.F., Troncoso-Palacios, J., Ferri-Yáñez, F., Lobos, G. (2013). *Liolaemus flavipiceus* Cei & Videla, 2003: primer registro en Chile y nuevos antecedentes para el taxón (Reptilia, Sauria, Liolaemidae). Cuad. Herpetol.

Apéndice 6.- Troncoso-Palacios, J., Ferri-Yáñez, F. (2013). *Liolaemus patriciaiturrae* Navarro and Núñez, 1993 (Squamata: Liolaemidae): Distribution extension in northern Chile and geographic distribution map. Check List.

Apéndice 7.- Troncoso-Palacios, J., Ferri-Yáñez, F. (2012). Revisión del estatus taxonómico de *Liolaemus Josephorum*. Núñez, Schulte & Garin 2001 (Iguania: Liolaemidae). Boletín del Museo Regional de Atacama.

ECOLOGY LETTERS

Ecology Letters, (2013) doi: 10.1111/ele.12155

REVIEW AND SYNTHESIS

Heat freezes niche evolution

Miguel B. Araújo,[1,2,3,*a] Francisco Ferri-Yáñez,[1a] Francisco Bozinovic,[4] Pablo A. Marquet,[4,5,6] Fernando Valladares[1] and Steven L. Chown[7]

Abstract

Climate change is altering phenology and distributions of many species and further changes are projected. Can species physiologically adapt to climate warming? We analyse thermal tolerances of a large number of terrestrial ectotherm ($n = 697$), endotherm ($n = 227$) and plant ($n = 1816$) species worldwide, and show that tolerance to heat is largely conserved across lineages, while tolerance to cold varies between and within species. This pattern, previously documented for ectotherms, is apparent for this group and for endotherms and plants, challenging the longstanding view that physiological tolerances of species change continuously across climatic gradients. An alternative view is proposed in which the thermal component of climatic niches would overlap across species more than expected. We argue that hard physiological boundaries exist that constrain evolution of tolerances of terrestrial organisms to high temperatures. In contrast, evolution of tolerances to cold should be more frequent. One consequence of conservatism of upper thermal tolerances is that estimated niches for cold-adapted species will tend to underestimate their upper thermal limits, thereby potentially inflating assessments of risk from climate change. In contrast, species whose climatic preferences are close to their upper thermal limits will unlikely evolve physiological tolerances to increased heat, thereby being predictably more affected by warming.

Keywords

Bioclimatic envelope models, biological invasions, climate change, CTmax, CTmin, evolutionary rates, lower thermal tolerance, niche conservatism, species distributions, thermal adaptation, upper thermal tolerance.

Ecology Letters (2013)

INTRODUCTION

There is a general expectation that climate, both at present and historically, governs the broadest outlines of species distributions. The degree to which climatic preferences of species and climatic tolerances are conserved across lineages is still a matter of debate, as rates of niche evolution and the mechanisms underlying them remain poorly known (e.g. Losos 2008). The assumption is that some significant degree of conservatism exists in the fundamental niche – the set of environmental states that permits species to persist (for recent review of niche concepts see Peterson *et al.* 2011) – which provides predictability across taxa, environmental dimensions and time frames, when species responses to abiotic variables are investigated from evolutionary and ecological perspectives (e.g. Jablonski *et al.* 2006; Romdal *et al.* 2013). Nonetheless, a growing number of analyses suggest that key traits affecting physiological tolerances, which contribute to setting the fundamental niche, show much variation in the extent of their conservatism. Compelling examples include little systematic environmental variation in the sum of effective temperatures for insect development, compared with much rainfall-related variation in desiccation resistance for the same group (e.g. Addo-Bediako *et al.* 2001), and, in *Drosophila*, differences among various traits in the scope of their variation (e.g. Kellermann *et al.* 2012a,b).

In keeping with the finding that some traits show much variation, adaptations to recent climate change have been reported in several taxa, mostly involving phenological adaptation to shifts in the timing of seasonal events (e.g. Visser 2008), but also involving changes in the geographical distribution of genetic polymorphisms (e.g. Umina *et al.* 2005). Recorded differences among climatic niches in the native and non-native ranges of invasive species have also led to the suggestion that niches might have evolved during the invasion process (e.g. Broennimann *et al.* 2007; Fitzpatrick *et al.* 2007). Notwithstanding, tests of niche conservatism (sensu Losos 2008; i.e. whether niches change more slowly than expected from Brownian motion evolution) with measures of overlap between climatic niches inferred using methods that relate geographical distributions of species to aspects of climate have one important limitation: the theoretical expectation of conservatism is justified for fundamental (abiotic) niches rather than for realized niches (Araújo & Peterson 2012).

Realized niches are a subset of the fundamental niche reduced by the effects of dispersal, biotic interactions, and, with animals, by aspects of behaviour that affect resource utilization (e.g. Peterson

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[1] *Departamento de Biogeografía y Cambio Global, Museo Nacional de Ciencias Naturales, CSIC & Laboratorio Internacional en Cambio Global CSIC-PUC (LINCGlobal), Calle José Gutiérrez Abascal, 2, 28006, Madrid, Spain*

[2] *'Rui Nabeiro' Biodiversity Chair, CIBIO, University of Évora, Largo dos Colegiais, 7000, Évora, Portugal*

[3] *Center for Macroecology, Evolution and Climate, University of Copenhagen, Universitetsparken 15, 2100, Copenhagen, Denmark*

[4] *Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile & Laboratorio Internacional en Cambio Global CSIC-PUC (LINCGlobal), Alameda 340, Santiago de Chile, Chile*

[5] *Instituto de Ecología y Biodiversidad (IEB), Casilla 653, Santiago, Chile*

[6] *The Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, NM, 87501, USA*

[7] *School of Biological Sciences, Monash University, Victoria, 3800, Australia*

**Correspondence: E-mail: maraujo@mncn.csic.es*

[a] *These authors contributed equally to this study.*

et al. 2011). Although these factors are constrained by traits that, themselves, are expected to be conserved over long periods of time, the realized niches emerging from interactions between traits and the environment are not expected to be conserved. For example, non-physiological mechanisms of adaptation, such as thermoregulatory behaviour used by ectotherms to regulate physiological performance (and allow survival beyond species thermal tolerance limits), are often labile. Simulations have shown that such behavioural adaptations can even constrain rather than drive evolution (Huey *et al.* 2003), thereby reinforcing conservatism of the fundamental niches; an outcome being borne out by empirical work (e.g. Marais & Chown 2008). Another extreme case of lability in factors influencing realized niches are changes in diet. Adélie penguins in Antarctica, e.g. were able to switch in <200 year from a diet mainly composed of fish to one predominantly based on krill (Emslie & Patterson 2007). Although several of the factors determining realized niches of species are unlikely to remain stable through time, tests of conservatism are typically based on measurements of the realized niche (e.g. Hof *et al.* 2010; Kozak & Wiens 2010). It follows that since realized niches generally represent subsets of the fundamental niche, and ecological conditions in different times or regions can lead to different occupation of the fundamental niche (e.g. Jackson & Overpeck 2000), shifts in realized niches are often likely to indicate that different portions of the fundamental niche are being occupied rather than that evolutionary changes in the fundamental niche have taken place.

The significant question thus remains of whether physiological adaptation to ongoing climate warming or conservatism of climatic tolerances is more likely. Answers to this question are important for several reasons. First, several studies have suggested that a suite of tropical to subtropical ectotherms may be close to their thermal safety margins, which, if exceeded, could lead to the extinction of several species (Deutsch *et al.* 2008; Huey *et al.* 2009; Clusella-Trullas *et al.* 2011). Population-level assessments of reptiles suggest that climate change-driven extinctions may already be occurring (Sinervo *et al.* 2010), while some studies suggest that tropical endotherms may be similarly at risk (Cooper *et al.* 2011). Meta-analysis for many different terrestrial organisms is also showing that distributions of species have recently shifted to higher elevations at a rate of 11 metres per decade, and to higher latitudes at a rate of 16.9 km per decade, thus compromising the ability of several species to adapt to ongoing climate change by tracking shifting climate suitability (Chen *et al.* 2011). Second, understanding the scope for niche evolution is critical because the assumption of little evolutionary change underlies many projections of climate change effects on species distributions, both in the past (e.g. Nogués-Bravo *et al.* 2008) and future (e.g. Garcia *et al.* 2012). Third, the extent to which niche evolution takes place is a fundamental question in biogeography and evolution, with strong implications for understanding the origin, diversification and distribution of life on earth, and fundamental differences therein between marine and terrestrial systems (e.g. Wiens & Donoghue 2004; Sunday *et al.* 2012; Romdal *et al.* 2013).

IS EVOLUTION OF CLIMATIC NICHES ASYMMETRIC?

Questions regarding the evolution of the fundamental niches are difficult to address for at least three reasons. First, measuring the fundamental niche of a species is challenging because the full set of dimensions that constitute a species' niche is unknown and is likely to vary from one species to another. Furthermore, interactions between dimensions of the niche, e.g. temperature and water, can modify the tolerance of species to individual niche dimensions in ways that are not always easily predicted (e.g. Crimmins *et al.* 2011). Second, experiments measuring aspects of the fundamental niche are expensive and time consuming, thus being typically limited to small numbers of species. Third, demonstrating changes in one aspect of the niche of a species might provide little information about potential evolutionary changes in other aspects thereof (e.g. Angilletta *et al.* 2003). Nonetheless, biophysical approaches are demonstrating that a limited suite of traits can readily characterize important aspects of the fundamental niche, and that many of these have to do with thermal biology (Porter & Kearney 2009; Kearney *et al.* 2010). Indeed, suggestions have recently been made that the stage on which ecological and evolutionary interactions play out should be termed the 'thermodynamic niche' (Kearney *et al.* 2013). In consequence, investigations of differential variation in traits underpinning thermal biology are starting to provide important insights into the extent to which fundamental niches might evolve, and what the consequences thereof are for species distribution modelling and for predicting species responses to climate change, especially in environments as different as those found in marine and terrestrial systems (e.g. Sunday *et al.* 2012).

For many terrestrial animals and plants, the upper and lower thermal limits to performance are significant components of the thermal niche (e.g. Larcher 1995; Pörtner 2001; Hoffmann 2010). Specifically, for a number of terrestrial animal ectotherms, it has been shown that upper and lower thermal tolerance limits covary to only a limited extent or do not do so at all (Addo-Bediako *et al.* 2000; Hoffmann *et al.* 2013). However, in others, stronger covariation exists (e.g. Calosi *et al.* 2010). In marine groups, such covariation is especially pronounced (Sunday *et al.* 2011), perhaps owing to oxygen limitation of thermal tolerance (Pörtner 2010). In consequence, while evidence of general patterns is emerging for ectotherm animals (e.g. Addo-Bediako *et al.* 2000; Sunday *et al.* 2011; Kellermann *et al.* 2012b; Grigg & Buckley 2013; Hoffmann *et al.* 2013), how extensive the asymmetry in variability of upper and lower tolerances is among terrestrial organisms, and what its implications are for niche evolution in particular have not been comprehensively explored across a wide range of terrestrial plants and animals.

VARIATION IN CRITICAL THERMAL LIMITS ACROSS TAXA

Here, we explore the extent of the asymmetry in upper and lower tolerances by examining standardized metrics of thermal tolerance for 2740 terrestrial ectotherm, endotherm, and plant species with data spanning distributions across the world (Fig. 1; for full description of the data see Tables S1–S6 and references provided in the supporting information). Because thermal tolerance metrics are not fully comparable across studies (both within and between biological groupings), data were subdivided and analysed separately for each metric.

For ectotherms, the first group (A) includes critical minimum temperatures (CT_{min}) and critical maximum temperatures (CT_{max}) matched for 129 reptile species, minimum lethal temperatures (LT_{min}) and CT_{max} matched for 26 amphibians, and CT_{min} and CT_{max} matched for 12 spiders and 40 insects (Sunday *et al.* 2011; Hoffmann *et al.* 2013). The second group (B) includes estimates of CT_{min} and CT_{max} matched for 38 insect species (from Deutsch *et al.*

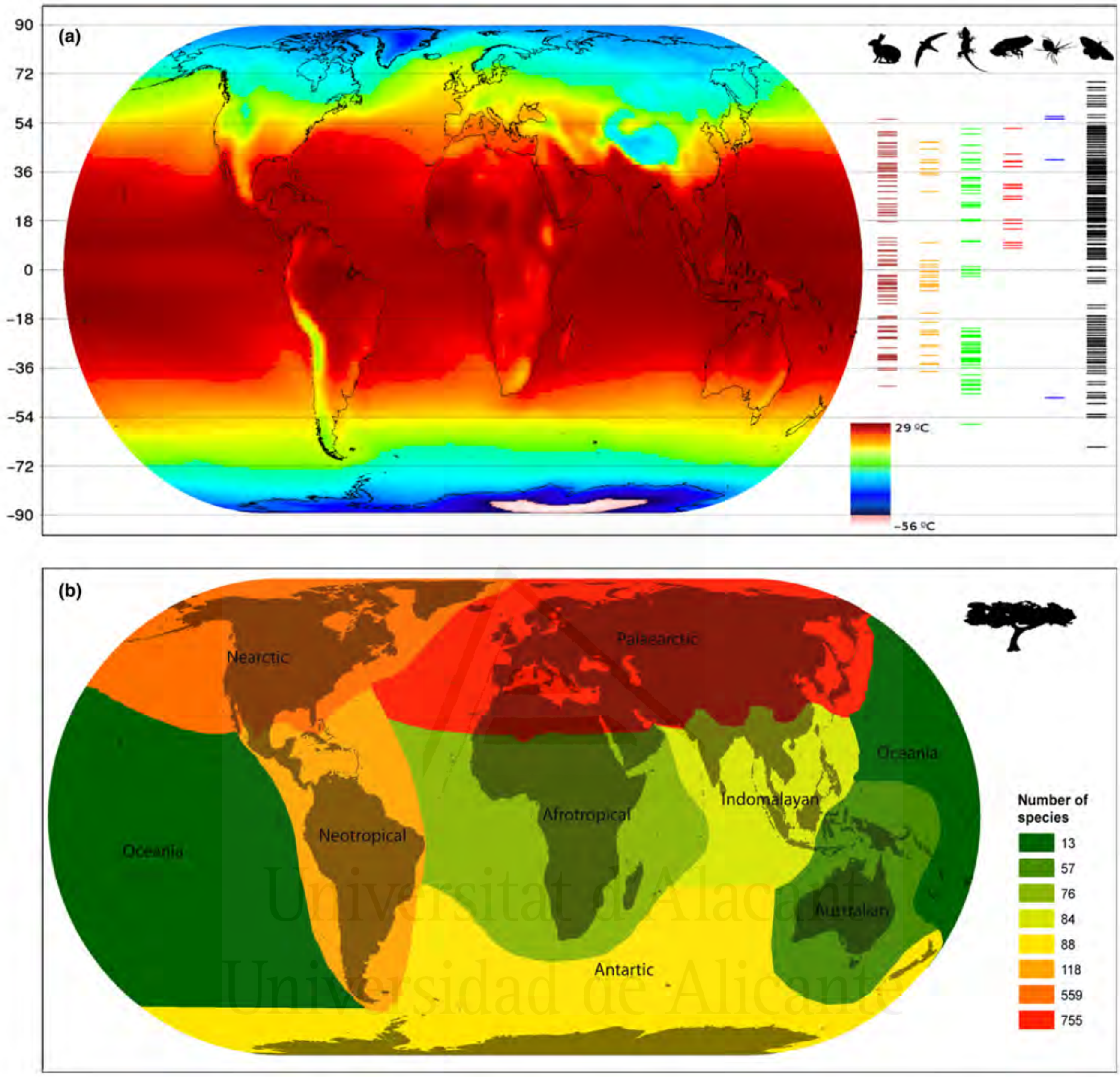

Figure 1 Distribution of the thermal tolerance data utilized in this study. (a) Colours depict annual mean temperature and bars on the right represent the centroids of species ranges calculated with data provided by Holt *et al.* (2013). Black bars are centroids of the range of insect species, spiders are represented with blue bars, amphibians are represented with red bars, reptiles are represented with green bars, birds are represented with orange bars and mammals are represented with brown bars. (b) Udvardy's plant Biogeographical Provinces of the World. Since maps of distributions of the plant species were not available for us, we assigned species to their native realms so that colours represent the number of species with thermal data per realm.

2008). Notice that the latter metrics are estimated from performance curves of the rate of development of organisms at different temperatures, so they are not directly comparable with other critical thermal measurements. The third group (C) includes a mix of metrics (CT_{min} and CT_{max}, lethal maximum and minimum temperatures in which 50% of the individuals die (LT_{min50} and LT_{max50}), and lethal maximum and minimum temperatures in which 100% die (LT_{min100} and LT_{max100}) for 704 insects (Kellermann *et al.* 2012b; Hoffmann *et al.* 2013). While the data sets A and B include upper and lower tolerances matched for each individual species, the third data set includes unmatched upper and lower thermal tolerances across species. These unmatched data provide a less powerful comparison, but due to the substantial sample size we elected to analyse them, while distinguishing these data from those where lower and upper tolerance metrics were matched for every species.

For endotherms, we reviewed 84 studies determining thermal neutral zone (TNZ) boundaries for birds and mammals, i.e. the range of external ambient temperatures in which the resting metabolic rate is constant and minimum (McNab 2012), and constructed a database of paired lower critical temperatures (LCT) and upper critical temperatures (UCT) for 227 species (see supporting information).

For plants, we reviewed 35 physiological studies using photosystem II (PSII), a protein complex that is related with the performance and survival of plants under extreme temperatures (e.g.

Valladares & Pearcy 1997). Non-destructive measurements of chlorophyll fluorescence, determining the maximal efficiency of PSII photochemistry (*Fv/Fm*) of the leaves, are recorded as temperatures are raised or lowered under controlled laboratory conditions (e.g. Gimeno *et al.* 2009). The critical temperature promoting a reduction of 50% of the initial *Fv/Fm* values (LT_{50}) is then obtained after fitting the corresponding response curves. This metric has been shown to correlate with other physiological estimates of thermal tolerance, such as membrane breakage and electrolyte leakage (Sierra-Almeida & Cavieres 2010), although lower performance limits may be set more by constraints on growth than on photosynthesis, at least for elevation tree lines (e.g. Hoch & Körner 2012). When data on LT_{50} were not provided in the papers reviewed, whenever possible we estimated it from alternative measures such as *T*c, the critical temperature, defined as the intersection of the lines extrapolated from the slow and fast rise portion of the temperature basal fluorescence response curve, which is highly correlated with LT_{50} (e.g. Zhang *et al.* 2012). Regression lines obtained from studies simultaneously reporting various parameters were used to estimate LT_{50} values from studies only providing values for these alternative parameters. Overall, LT_{50} values were obtained for 520 plant species, 64% of them for cold tolerance, 36% for heat tolerance, with paired data representing only 4% of the total ($n = 19$). Estimates of cold tolerance were also available for a large number of plant species, specifically cold hardiness ($n = 1190$) and frost tolerance ($n = 106$), but no analogue measurements were found for heat tolerance. The latter is typically expressed as number of days above 30 °C that a species is able to tolerate, but not as absolute temperature. Thus, results regarding these tolerance measures are provided in the supporting information.

Regarding ectotherms, more specifically reptile species from group A, we found that CT_{max} averaged 42.2 °C with variance 8.3, whereas CT_{min} was 7.8 °C with variance of 13.5 (Fig. 2a). Similar differences between CT_{max} and LT_{min} were found for amphibians, with twofold increases in the variance of tolerance to heat vs. cold (11.3 vs. 20.7), and for spiders with sixfold increases of variance (2.6 vs. 16.7) (Fig. 2a). For insects, we recorded almost twofold increases of variance (29.0 vs. 41.1) with data from group A (Fig. 2a), and roughly the same with group B (13.8 vs. 30.6) (Fig. 2b). With the unmatched lower and upper tolerance values with data from group C (Fig. 2c) the same general pattern emerged (variance of lower tolerance = 142.2 with $N = 254$, and variance of upper tolerance = 37.9 with $N = 371$), with lethal minimum temperature values extending far below any CT_{min} measurement for ectotherms (Fig. 2a and b) and below LT_{min} values reported for amphibians (Fig. 2a).

To explore the prediction that intraspecific niche variation is also lower near the critical thermal maximum than near the thermal critical minimum, we analysed data from 29 species of South American

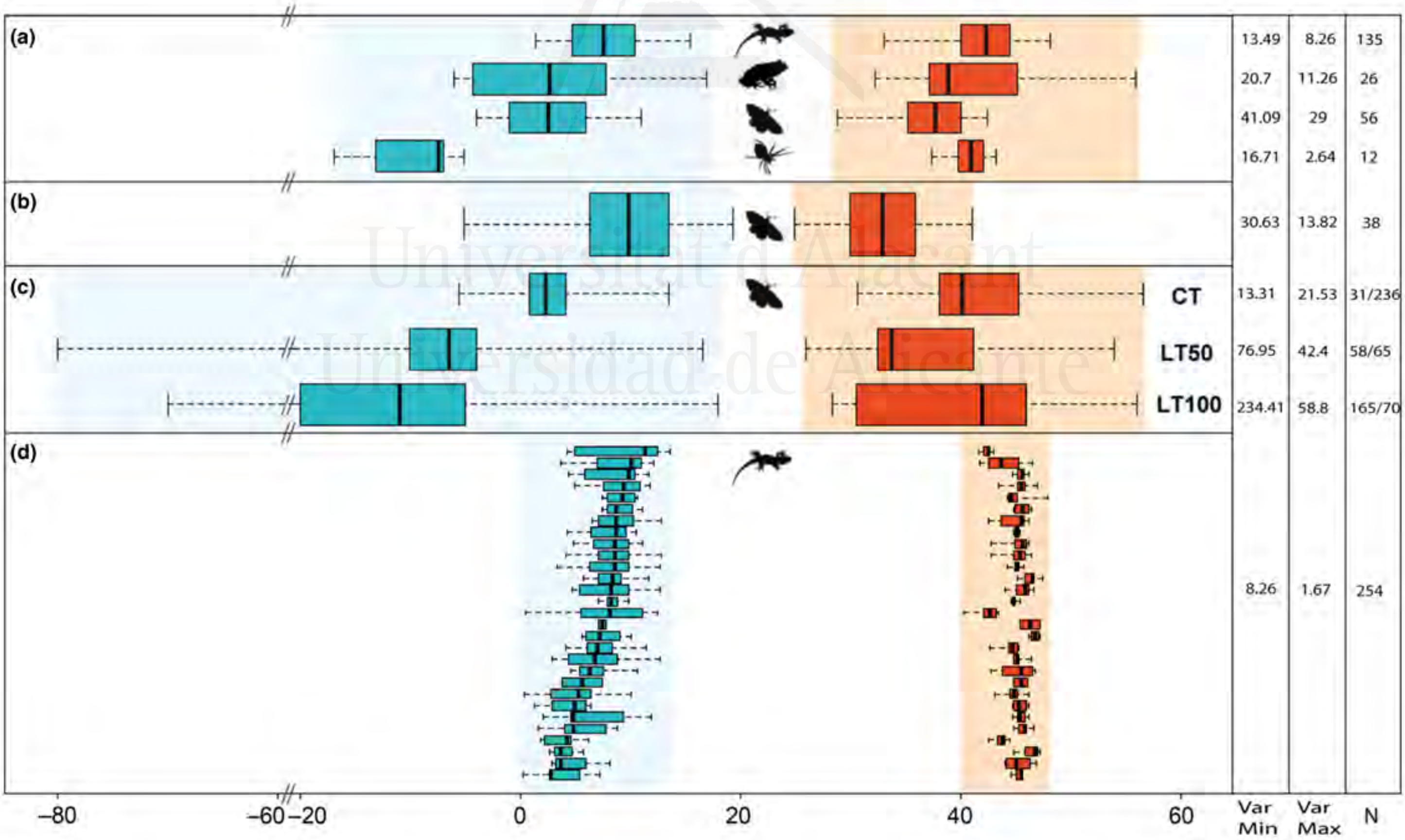

Figure 2 Variance of cold tolerance (green plots, left) vs. heat tolerance (red plots, right) among terrestrial ectotherms. (a) Box plots of CT_{min} and CT_{max} for 135 species of reptiles and LT_{min} and CT_{max} for 26 species of amphibians, and CT_{min} and CT_{max} for 12 spiders and 56 insects (Sunday *et al.* 2011; Hoffmann *et al.* 2013); (b) Box plots of CT_{min} and CT_{max} for 38 species of insects (data from Deutsch *et al.* 2008); (c) Box plots of a mix of unmatched lower and upper CT and LT values for 459 insects (Kellermann *et al.* 2012b; Hoffmann *et al.* 2013); (d) Box plots of CT_{min} and CT_{max} for 29 *Liolaemus* lizard species (each one of the 29 boxes represents intraspecific variation among individuals of the same species) in Chile (F. Ferri-Yáñez, unpublished data).

Liolaemus lizards from Chile for which several individual replicates exist for different species (mean number of individuals per species 9 ± 4.2, unpublished data from F. Ferri-Yáñez, see details on the methods for data collection in the supplementary material). Results of intraspecific variation of thermal niche traits for the Chilean lizards were consistent with interspecific variability found among other ectotherms, i.e. lower for intraspecific CT_{max} than for CT_{min} (Fig. 2d). Critical maximum temperatures (CT_{max}) among *Liolaemus* species averaged 45.0 °C (Variance = 1.7) and critical minimum temperatures (CT_{min}) averaged 7.4 °C (Variance = 8.3) (Fig. 2d).

The same pattern of asymmetric variation in lower and upper thermal tolerances for ectotherms was recorded for endotherms and plants. Mean L_{CT} and U_{CT} for birds were 24 and 35 °C, respectively, with estimates of cold tolerance being more than four times as variable as heat tolerance (Fig. 3a). For mammals, average L_{CT} and U_{CT} were 26 and 34 °C, respectively, and variances of L_{CT} were more than seven times larger than variances of U_{CT} (Fig. 3b).

For plants, the differences in variance were even more striking. For the subset of species with paired measurements of cold and heat tolerance (Fig. 4a), mean critical values were −20 and 46 °C for cold vs. heat tolerance and variances were almost 24 times greater for cold tolerance than for heat tolerance. For the species with unpaired measurements, mean critical values were −12 and 47 °C, and variances were five times greater for critical tolerances to cold than to heat (Fig. 4b). Even greater variances existed for measurement of frost tolerance and cold hardiness (Fig. S2), but no analogue metrics were available for upper limits.

VARIATION IN CRITICAL THERMAL LIMITS ACROSS ENVIRONMENTAL GRADIENTS

Given the asymmetry in variation of lower and upper thermal limits found in previous analyses (e.g. Addo-Bediako *et al.* 2000), and stronger relationships between lower limits and latitude than between upper limits and latitude (e.g. Sunday *et al.* 2011), we expected that a positive correlation should exist between lower thermal limits and ambient temperature. Likewise, a much weaker relationship should be expected for upper thermal limits and ambient temperature. In other words, if tolerances to low temperatures are highly labile and lability is driven by natural selection, species exposed to low temperatures should have a tendency for greater tolerance to cold, while species not exposed to low temperatures should have a tendency for reduced tolerance to cold. In contrast, if tolerances to high temperatures are highly conserved across clades, natural selection might not be expected to be acting as strongly on this trait, resulting in a weak relationship. We examined these expectations by plotting physiological metrics of critical tolerance (CT_{max} and CT_{min} for ectotherms and U_{CT} and L_{CT} for endotherms) against metrics of ambient temperature averaged across species ranges. Plotting biological patterns against measured environmental gradients is generally preferable to plotting them as general geographical clines (i.e. as a function of latitude or altitude), as the latter are usually only indirectly, and often differently, related to the various environmental measures that are of biological significance (see for discussion Hawkins & Diniz-Filho 2004; Korner 2007). We also compensated for the allometric relation between L_{CT} and mass (McNab 2012), by fitting a linear model of L_{CT} with the log-transformed body weight in mass and using the residuals to assess the relationship with ambient temperatures.

The ambient temperature metrics we selected are commonly used in modelling studies of species distributions (e.g. Peterson *et al.* 2011) and include the following: minimum temperature of the coldest month (T_{min}), maximum temperature of the warmest month (T_{max}) and mean annual temperatures (T_{mean}). The analysis comparing upper and lower thermal limits against ambient temperatures was only possible for a subset of the species in our database with both physiological data and geographical distributional data, i.e. 64 reptiles (geographical data from www.iucnredlist.org), 38 insects

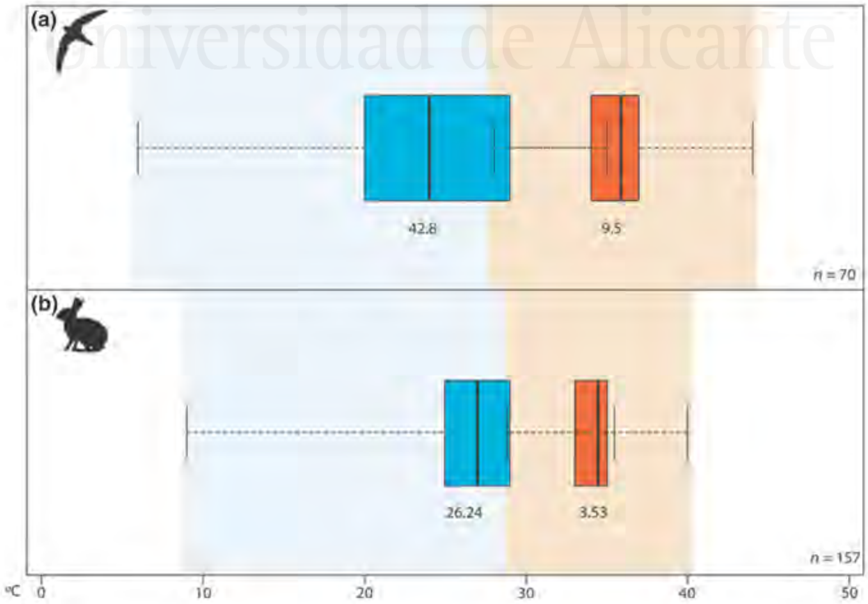

Figure 3 Variance of cold tolerance (green plots, left) vs. heat tolerance (red plots, right) for endotherms. Variances are depicted below every boxplot, number of species (*n*) is on the lower right section of the graph.

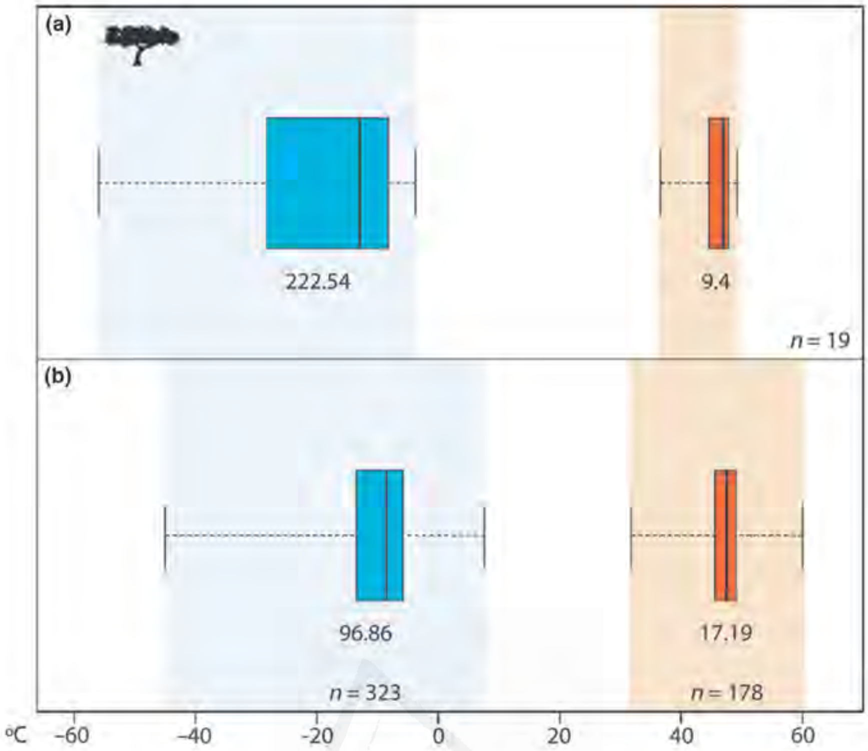

Figure 4 Variance of cold tolerance (green plots, left) vs. heat tolerance (red plots, right) among terrestrial plants. Physiological estimates of plant cold tolerance and heat tolerance (LT_{50}) are provided for (a) paired data and (b) unpaired data.

(from Deutsch *et al.* 2008) and 24 amphibians, 43 birds and 137 mammals (from Holt *et al.* 2013).

As expected, for ectotherms, we found that positive correlations exist between CT_{min} and averaged ambient temperatures (Fig. 5a, for correlations and *P*-values see Table S5). Although the strength of the correlations varies with taxonomic group, the relationship is positive for all. In contrast and consistent with our expectations, we found no clear pattern of correlation between CT_{max} and ambient temperatures (Fig. 5a). For example, for reptiles the correlation between CT_{max} and metrics of ambient temperature is markedly negative leading to the suggestion that adaptation to heat among these species might be driven by more complex relationships with a variety of climate variables (see discussion in Clusella-Trullas *et al.* 2011; Grigg & Buckley 2013). Indeed, most species have similar tolerances to heat (42 °C) and this is independent of the environments they are exposed to (e.g. *Zootoca vivipara* is exposed to T_{min} across the range of −20 °C and the species has as CT_{max} of 43.9 °C, whereas *Sphaerodactylus klauberi* is exposed to T_{min} of 16 °C and has CT_{max} of 36.3 °C). For amphibians, the correlation is either close to zero (with T_{mean}), clearly positive (for T_{max}), or slightly negative (for T_{mean}). For insects the correlation is positive but weak for all three metrics (i.e. always below $\rho = 0.35$).

For endotherms, there is an apparent lack of correlation between thermal limits and ambient temperature (Fig. 5b, for correlations and *P*-values see Table S6). The exception is T_{max} for which positive correlations with L_{CT} and U_{CT} were found for birds. A weak positive correlation was also found for U_{CT} in mammals ($\rho = 0.25$). However, when compensating for body mass (residuals L_{CT} in Fig. 5b) there is a significant correlation between cold tolerance and temperature, which is stronger for T_{max} $\rho = 0.414$). For birds, T_{max} also correlates with residuals of cold tolerance ($\rho = 0.380$). In other words, we found partial support for the prediction that natural selection might be driving physiological responses of mammals and birds to changes in ambient temperature (evidence for birds is restricted to T_{max}). In contrast, limited evidence supports that the physiological adaptation to heat is constrained by the environment with the exception of T_{max} for which a weak signal of adaptation was detected.

The most prominent feature of the above analysis is that, as expected, CT_{min} and L_{CT} tend to have a positive relationship with ambient temperature. By and large, ectotherm and endotherm species living in cold environments tend to be more tolerant to cold than ectotherm and endotherm species living in warm environments. Also, as predicted, species with greater tolerances to heat are not necessarily restricted to warmer environments. Correlations of CT_{max} and U_{CT} with ambient temperature were either close to zero, weakly positive or negative. Nonetheless, a consistent tendency for a positive correlation between T_{max} and upper thermal limits among ectotherms (except for reptiles) and endotherms was found. This is because some of the species with greater tolerances to high temperatures do live in the warmest environments (but species with great tolerances to heat are also found in colder zones). If this tendency were to be broadly confirmed it would indicate that some degree of selection, even if weak, might be occurring for upper thermal limits in warmer environments (but always below 50 °C, see following discussion on 'hard' physiological limits). Further exploration of this idea, and the general tendencies we have confirmed here building on previous work (Addo-Bediako *et al.* 2000; Clusella-Trullas *et al.* 2011; Sunday *et al.* 2011), is clearly required, especially taking more explicit account of phylogenetic correlation. Although we did not

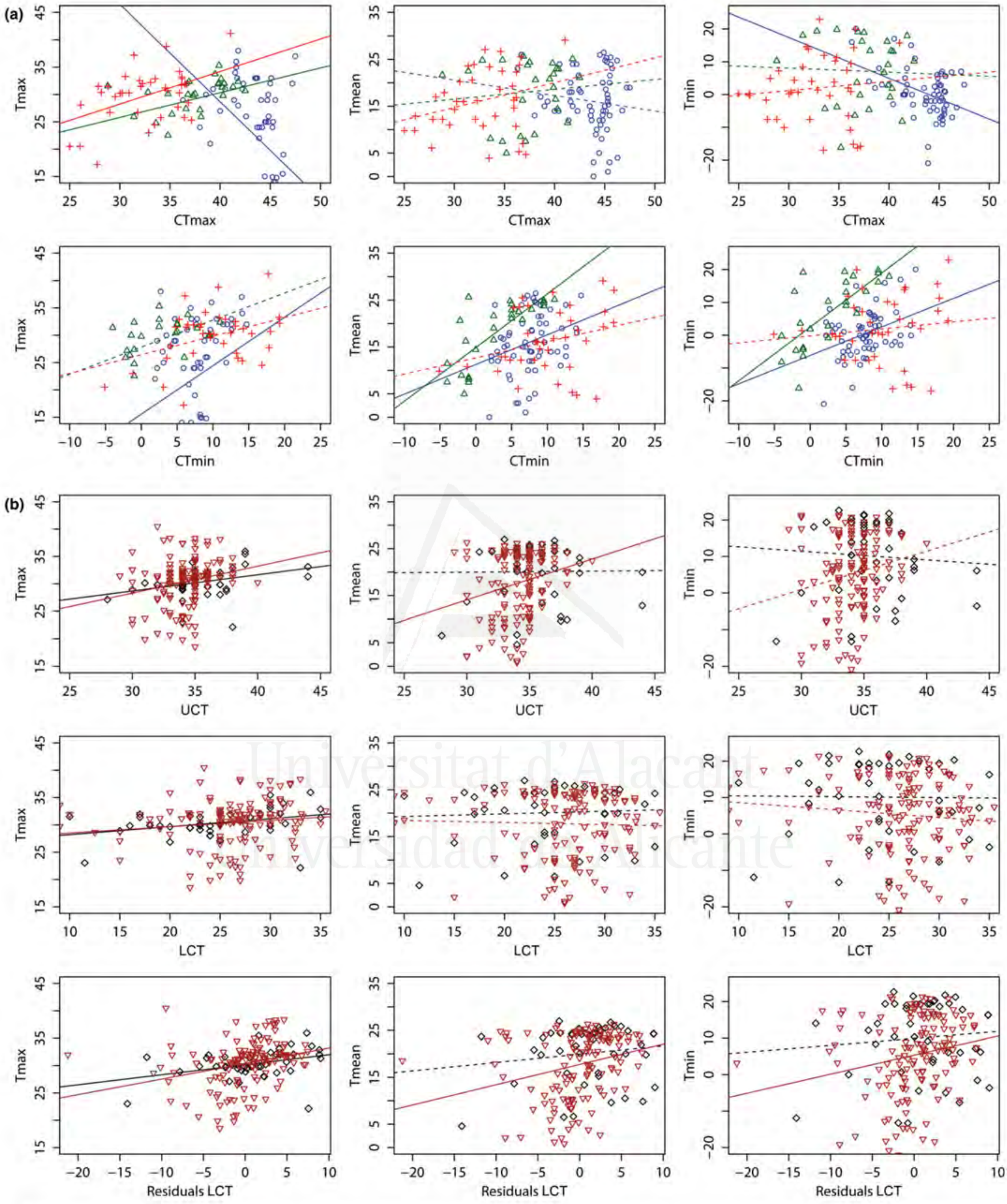

Figure 5 Scatter plots and regression lines between thermal tolerances and ambient temperatures for 64 species of reptiles (Blue circles), 26 species of amphibians (green triangles), 38 species of insects (from Deutsch *et al.* 2008; red crosses), 43 species of Birds (black squares) and 137 species of mammals (brown inverse triangles). T_{mean}: yearly mean temperature, T_{max}: Maximum temperature of warmest month and T_{min}: minimum temperature of coldest month (from Hijmans *et al.* 2005). CT_{max}: critical thermal maximum, CT_{min}: critical thermal minimum (Lethal Thermal minimum for amphibians), UCT: upper critical temperature for endotherms, LCT: lower critical temperature for endotherms. The residuals of regressing body mass and LCT in endotherms are plotted (Residuals LCT).

do so here, for reasons of disparate taxa and lack of phylogenies covering them, our findings are consistent with those of previous investigations, which have used a variety of approaches, and all of which have resulted in similar conclusions (e.g. Sunday *et al.* 2011, 2012; Hoffmann *et al.* 2013).

WHY WOULD EVOLUTION OF CLIMATIC NICHES BE ASYMMETRIC?

Our synthetic overview, and further analyses, unequivocally show that variation in thermal tolerances among terrestrial organisms is asymmetric (for syntheses of results see also Fig. S1). Specifically, a remarkable contrast of variability exists between interspecific tolerances to cold vs. heat among a large sample of terrestrial ectotherm, endotherm and plant species. The pattern also appears to hold true when intraspecific tolerances to cold vs. heat are measured among a small number of *Liolaemus* lizard species in South America. These results extend, to a wide variety of organisms, the finding for some terrestrial ectotherms that, generally, lower thermal limits are far more labile than upper limits (e.g. Addo-Bediako *et al.* 2000; Boher *et al.* 2010; Sunday *et al.* 2011; Grigg & Buckley 2013; Hoffmann *et al.* 2013). For a smaller set of ectotherm and endotherm species, we also show that critical limits to cold tend to correlate with metrics of ambient temperature, thus supporting the hypothesis that natural selection modulates physiological adaptation of species to lower temperatures. In contrast, critical limits to heat are, by and large, uncorrelated with metrics of environmental temperature partially supporting the hypothesis of conservatism of physiological tolerances to heat. These results also broaden previous evidence provided for terrestrial ectotherms that lower thermal limits are generally correlated with latitude (an indirect variable expected to correlate with metrics of ambient temperature), whereas upper thermal limits show much less geographical variation (e.g. Addo-Bediako *et al.* 2000; Sunday *et al.* 2011; Grigg & Buckley 2013). In consequence, they also implicitly suggest that the differences in range dynamics among marine and terrestrial species in response to changing climates, that have been identified previously on the basis of different asymmetries in tolerance (Sunday *et al.* 2012), may extend more broadly.

It might be argued, however, that phenotypic plasticity could reduce the extent of the differences in lability of upper and lower thermal tolerances. However, for a wide range of ectotherms evidence is accumulating that plasticity of upper limits is much reduced by comparison with plasticity of lower limits (see also Chown & Terblanche 2006; Hoffmann *et al.* 2013). How common this is for endotherms and plants is not yet clear, although it deserves explicit investigation for reasons that will become clear below (see also Piersma & Drent 2003).

Asymmetry in conservatism of lower and upper thermal limits is likely to be the consequence of different physiological processes operating near critical lower and upper thermal limits. With animals, variation in lower thermal limits is a consequence of differences in thermodynamic effects of temperature on reaction rates, and most likely those responsible for maintaining ion homeostasis (e.g. Hosler *et al.* 2000; MacMillan *et al.* 2012). In contrast, variation in tolerance to heat is mostly a consequence of limited variation in the ability of organisms to counter the destabilizing effects of high temperature on membranes and proteins (for review see Angilletta 2009). The latter processes involves, *inter alia*, ancient polypeptides that are expected to be highly conserved across all forms of living organisms (e.g. Gupta & Golding 1993).

Likewise, cold acclimation of plants relies on adjusting metabolic processes (essentially photosynthesis and respiration) and on avoiding lethal freezing (e.g. Larcher 1995). Both aspects have been shown to be highly dynamic since plants not only adapt quickly to thermal environments but also acclimate and de-acclimate seasonally to low temperatures (e.g. Pagtera & Arorab 2013). Plants have also been shown to acclimate quickly to high temperatures (e.g. Sung *et al.* 2003). However, changes in lipid composition of the membranes and increased production of heat shock proteins, two basic processes involved in heat tolerance of plants, are typically not sufficient to enable them to cope with temperatures above 45 °C, except in exceptional circumstances, such as in the case of desiccated state of resurrection plants (e.g. Larcher 1995; Kappen & Valladares 2007). Thus, as is the case with animals, sound physiological reasons exist to explain why plants are more likely to exhibit higher variability and adaptive potential in their lower rather than their upper limits of thermal tolerance.

Higher order processes likely set thermal limits in marine organisms (Pörtner 2001), often resulting in close matches between range limits and thermal tolerances, with important consequences for range dynamics (Sunday *et al.* 2012). Although higher order processes have also been claimed to set thermal limits in terrestrial ectotherms (Pörtner 2001), several studies suggest that the latter is unlikely (e.g. Klok *et al.* 2004; McCue & Santos 2013). These profound differences between marine and terrestrial groups may partly account for the differences in the associations between ranges and tolerances found in marine and terrestrial organisms, with 'mismatches' being more common in terrestrial species (see the detailed treatment of tolerances, range filling and the impacts of climate change by Sunday *et al.* 2012).

Clearly, some organisms are able to develop substantial resistance to high temperatures, but this is rare (reviewed by Hoffmann *et al.* 2013). For example, lichens, bryophytes and vascular plants can increase their heat tolerance, with some species being able to recover from temperatures exceeding 80 °C and even 120 °C if these are experienced in desiccated state (e.g. Kappen & Valladares 2007). The same is true of some of several anhydrobiotic invertebrates (e.g. Watanabe *et al.* 2002). Perhaps, most notable are extremophilic microbes whose proteins can be synthesized at temperatures exceeding 100 °C (e.g. Kashefi & Lovley 2003). Several desert ant species are also known to tolerate temperatures exceeding 50 °C during short-term periods of activity (e.g. Wehner *et al.* 1992). However, the average upper thermal limit for insects in our data is 41.6 °C and temperatures above 47.8 °C are thought to be tolerated only temporarily by animals (Pörtner 2002).

In this context, an important question is whether complex terrestrial organisms can evolve hyperthermostability (the ability to maintain structural stability and function at high temperatures e.g. >50 °C) under specific circumstances. Forecasts are for ongoing increases in global temperatures that will, in many circumstances, exceed organismal upper thermal limits substantially constraining fitness (and ultimately survival) (e.g. Wahid *et al.* 2007; Kearney *et al.* 2009; Bozinovic *et al.* 2011). If organisms are unlikely to be able to alter upper thermal limits, by whatever mechanism, then extinction risk may be much higher than currently anticipated. However, behavioural regulation and microclimate availability may still provide important opportunities for improvement of performance and survival.

Ultimately, the question is whether conservatism of upper thermal tolerances among terrestrial organisms is due to hard physiological boundaries that prevent adaptation of organisms beyond given temperature limits, whether it is due to biogeographical legacies that set the context for evolution, or whether selection for tolerance of rare temperature events might be responsible for it. The biogeographical argument is as follows: Earth's climate has been predominantly warm throughout its history with pulses of cold climates coming and going (e.g. Ruddiman 2001). The planet was at its coldest known state between 850 and 550 million years ago (mya), and complex organisms evolved after this period (e.g. Romdal *et al.* 2013). Subsequently, two major glaciations occurred: the first between 325 and 240 mya; and the second at 35 mya, at the onset of the Oligocene. A shorter glaciation might have also taken place at about 430 mya (Ruddiman 2001). However, the critical issue for evolution is that the equatorial region has remained warm through glacial-interglacial cycles (between 30 and 40 °C between the Paleocene and the Pliocene, Fig. 6), while higher latitudes were exposed to marked climatic variation (from nearly 0 to −80 °C, Fig. 6). Thus, it is not surprising that the vast majority of clades evolved in the thermally stable and warm equatorial region (e.g. Jablonski *et al.* 2006; Romdal *et al.* 2013), while some clades were able to colonize higher latitudes via physiological adaptations to lower temperatures (e.g. Wiens & Donoghue 2004).

If the world remained warm during most of its history, with most species evolving in environments exposed to relatively high temperatures, better performance at higher temperatures (a thermodynamic effect – e.g. Asbury & Angilletta 2010) would be expected, and maximum performance temperatures would also be closer to thermal maxima than thermal minima, owing to irreversible enzyme inactivation at higher temperatures (i.e. thermal responses would be negatively skewed, as is the case – see Kingsolver 2009). Opportunities for speciation and evolution of thermal niches would thus occur through adaptive radiation in relatively colder and species poor areas (e.g. Gavrilets & Vose 2005). This reasoning could explain why most selective pressures favoured niche evolution in cold environments while little pressure existed for evolution of thermal niches in warm and stable environments (Donoghue & Moore 2003). However, it does not explain why so little evidence exists for thermal evolution above 50 °C.

Hard physiological boundaries, or selection for survival of rare, high extreme temperature at any latitude (absolute maximum temperatures vary much less across space than do absolute minima – see Addo-Bediako *et al.* 2000) are, at this stage, the two most plausible alternative explanations for conserved upper thermal limits. Distinguishing among these alternatives has not been the subject of detailed research. However, the former is, in our view, most plausible given that so few metazoan organisms, even in extreme environ-

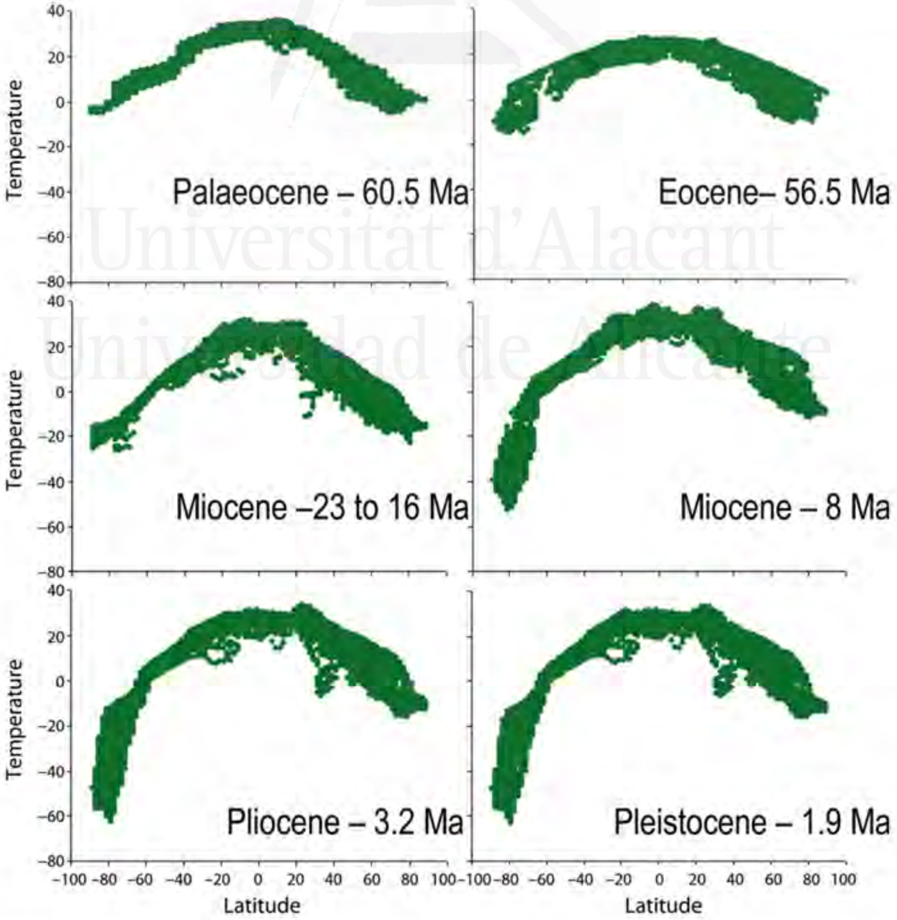

Figure 6 Changes in mean annual temperature values (°C) across latitude from the Paleocene to the Pliocene. Raw data to build the figure were based on GCM simulation hindcasts kindly provided by Persaram Batra (Miocene 23–26) and Paul Valdes and Alan Haywood (Palaeocene, Eocene, Miocene 8, Pliocene 3.2 and 1.9).

ments such as at marine hydrothermal vents (e.g. Ravaux *et al.* 2013), are able to exploit exceptionally hot, though energy rich, environments (i.e. much above 50 °C). Nonetheless, it is clear that explicit consideration of these alternatives is an important area for research.

Indeed, given that a few metazoans and plants seem to have evolved mechanisms to overcome temperature extremes (see above, and also Girguis & Lee 2006), understanding the biochemical and genetic basis of this ability, and how it might be promoted in other groups, is clearly important for the further development of conservation strategies for adapting to ongoing global temperature increases. Research on a variety of taxa is starting to address this question, especially from a genetic perspective, but consensus has yet to emerge (see Williams *et al.* 2012 for a brief overview). If upper thermal tolerance boundaries are indeed hard (or show limited ability to evolve), and the prospects for dispersal keeping pace with rates of change limited, then assisted migration (or managed relocation) may indeed become a preferred strategy, irrespective of its potential risks (e.g. Schwartz *et al.* 2012). In contrast, if upper boundaries are more malleable and can be altered through hybridization of populations or other approaches that might be considered a form of 'assisted evolution', then alternatives to wholesale relocations are plausible. Assisted evolution of domestic species has been a key component of human success, but has rarely been applied in this form in a conservation context (but see e.g. Jones & Monaco 2009).

NICHE CONSERVATISM LEADS TO NICHE SIMILARITY

High conservatism of upper thermal limits among terrestrial organisms suggests that many species are unlikely to evolve physiological tolerances to increased heat, especially when their climatic preferences are close to their upper thermal limits. In such cases, evolution of physiological tolerances will be impaired, and species persistence challenged unless species have other means to adapt to increased environmental temperatures – a topic now being thoroughly investigated (Deutsch *et al.* 2008; Huey *et al.* 2009; Clusella-Trullas *et al.* 2011; Kellermann *et al.* 2012b; Sunday *et al.* 2012; Grigg & Buckley 2013; Hoffmann *et al.* 2013). But another, more general and largely unnoticed consequence of niche conservatism is that fundamental niches, or at least the thermal components of the fundamental niches, are likely to be more similar among closely related species than is usually inferred with methodologies that relate geographical distributions of species with aspects of climate.

The idea that tolerances of species to environmental gradients varies continuously along those gradients was first proposed by Whittaker (1967). His ideas led to the development of the theory of gradient analysis and the continuum concept in community ecology, whereby species should gradually substitute each other along environmental gradients due to varying individual preferences and tolerances (see also Austin 1985). Even though these ideas were developed based on extensive empirical analyses of plant species distributions, we show here that the type of response curves of species in relation to the environment that were obtained for plants (e.g. Whittaker 1967) are unlikely to be fundamentally different from the response curves obtained for animals (see Fig. 7a). Indeed, the generality of such relationships has meant that the continuum concept underlies much of the thinking that motivates bioclimatic envelope modelling (alternatively termed ecological niche modelling, habitat suitability modelling, or species distribution modelling; see for recent review of terminology Araújo & Peterson 2012), and that is used to infer species climatic niches based on associations between aspects of climate and species' geographical distributions (e.g. Austin 1985; Peterson *et al.* 2011). As shown in Fig. 7b, however, niche conservatism can cause the metabolic (thermal) response curves of different species to be more similar than expected if climatic niches were inferred from analysis of geographical distributions and species occupancies of thermal gradients. Although varying levels of conservatism might exist among traits affecting different dimensions of the fundamental niches (e.g. tolerance to water), our extensive analysis of lower and upper thermal limits among terrestrial organisms is consistent with the proposition that fundamental niches, or at least their thermal component, should be more similar among species than typically inferred with methods that relate the geographical distributions of species with their environment.

Even though interspecific and intraspecific differences between fundamental niches are expected due to niche evolution and/or phenotypic plasticity (see also e.g. Hoffmann *et al.* 2003; Klok & Chown 2003), we expected the thermal component of the fundamental niches to differ less within and among species than the thermal component of realized niches. Moreover, major interspecific and intraspecific differences between fundamental niches should be expected mainly at the tails of the species-temperature response curves, especially when these tails approach lower temperature limits (Fig. 7b). In contrast, limited overlap between realized niches of closely related species is likely to be more common and a consequence of historical climatic legacies (e.g. Ricklefs 2006), the effects of biotic interactions (e.g. Dobzhansky 1950), limited dispersal (e.g. Baselga *et al.* 2012) and, perhaps, variation in species tolerances to aspects of the environment that are not characterized by, but may also influence responses to thermal gradients.

CONSEQUENCES OF NICHE SIMILARITY FOR STUDIES IN ECOLOGY AND EVOLUTION

The extent to which functional traits, performance currencies, and the environment, vary across clades is a central question in ecology and evolution (e.g. Messier *et al.* 2010). Our prediction that fundamental niches are more similar across lineages than inferred from analysis of realized niches is of critical importance for a range of research questions. For example, uncritical analysis of realized climatic niches can lead to important mistakes when predicting the effects of climate change on species distributions, assessing the risk of species invasion, or making inferences about rates of niche evolution. Specifically, if realized niches are highly constrained by dispersal, biotic interactions, and/or resource utilization, as they are expected to be at low latitudes and altitudes (e.g. Dobzhansky 1950; Loehle 1998), then they are unlikely to provide accurate estimates of species tolerance limits to climate. When this is the case, projections from bioclimatic envelope models will have a tendency to overestimate the effects of climate change on species distributions, underestimate the risk of species invasions, and miscalculate rates of niche evolution. In contrast, if realized niches are mainly constrained by climate variables, as it expected to be the case at higher latitudes and altitudes, then greater similarity between realized niches and fundamental niches is expected with the consequence that bioclimatic envelope models are also more likely to provide

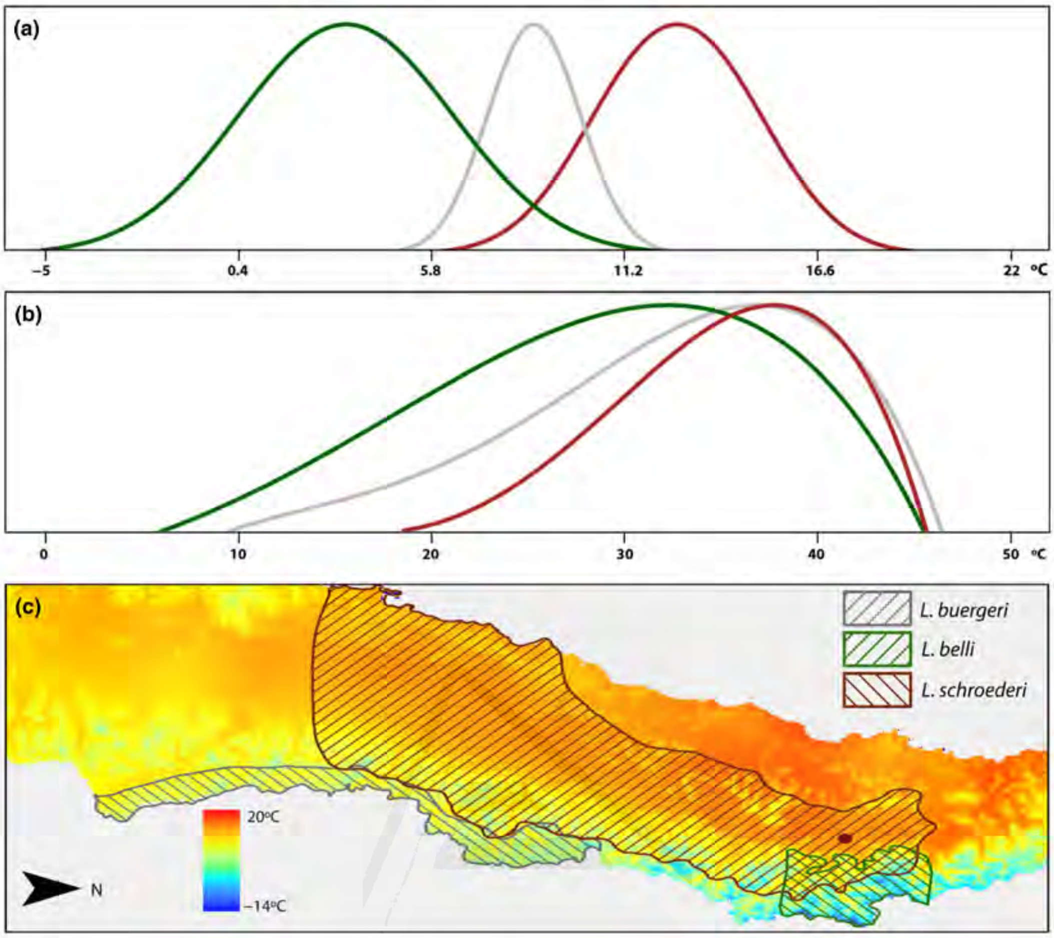

Figure 7 (a) Response curves estimated with bioclimatic envelope models (logistic regression) relating species distributions of three species of *Liolaemus* lizards in central Chile (see panel c) against mean annual air environmental temperatures (from Hijmans *et al.* 2005) (i.e. characterization of the realized niche for mean annual temperature); (b) empirical performance curves for the same species of *Liolaemus* (from F. Ferri-Yáñez, unpublished data) measured with sprint speed in laboratory conditions against body temperature (i.e. characterization of the fundamental niche for body temperature); and (c) geographical distributions of the three species of *Liolaemus* (from P.A. Marquet and C. Garin, unpublished data) overlaid on mean annual temperature.

accurate predictions. This outcome is most likely when thermal aspects of the environment–organism interaction are most significant, which is in any case often the outcome of many bioclimatic envelope models given the significance of the thermal environment for organisms (e.g. Walther *et al.* 2005; Kearney *et al.* 2010). Rates of environmental change may also play a role given differential organismal responses to them, particularly phenotypic plasticity (e.g. Terblanche *et al.* 2011), although plasticity is much less significant for upper thermal tolerance traits (see above).

Among work done recently, a comprehensive example of the significance of understanding fundamental thermal limits in the context of species distributions is provided by Sunday *et al.* (2012). They show how differences in the way upper and lower thermal limits vary among marine and terrestrial organisms have fundamental implications for understanding species distributions as climate continue to change. The *Liolaemus* lizards discussed above (see Fig. 7) provide a further example. Assume, for the sake of argument that a reasonable and similar correlation exists between increases in ambient temperature and increases in the body temperature of the species. If ambient temperatures increased uniformly across the gradient, populations of *Liolaemus schroederi* at the upper tail of the temperature gradient would be the first to go extinct unless behavioural adaptations enabled them to persist under further warming (e.g. Huey *et al.* 2003). Assuming a similar interspecific relation between ambient and body temperatures, bioclimatic envelope models would be expected to correctly predict extinctions because the upper tail of the species-temperature response curve inferred with bioclimatic envelope models (Fig. 7a) as the lizard temperature reaches the upper thermal tolerance of the species as measured under laboratory conditions (Fig. 7b). In contrast, mismatches between the upper thermal tolerances and the upper tails of the species-temperature response curves, as is clear for the other two species, would cause failure of models to predict correctly extinctions under warming. For example, increased temperatures along the thermal gradient in Fig. 7b would cause bioclimatic envelope models to shift to the right and predict losses of climate suitability within existing ranges of *Liolaemus belli* and *Liolaemus buergeri*. However, if species are exposed to temperatures below their preferred body temperatures, increases in ambient temperature will increase their fitness. That is, models inferring niches from assessments of the relationship between geography and the environment would have a tendency to overestimate extinction risk in a climate warming scenario.

When realized niches for closely related species are segregated along the temperature gradient (Fig. 7a) and thermal fundamental niches are overlapping for them (Fig. 7b), one implication is that several regions with suitable climate for the species are likely to be unoccupied. A low degree of equilibrium of species distributions with climate has already been reported for ectotherms (e.g. Munguía *et al.* 2012), endotherms (e.g. Monahan & Tingley 2012) and plants (e.g. García-Valdés *et al.* 2013), and one of the consequences for modelling of invasive species outside of their native ranges is that models will underestimate the extent of the areas that can be invaded. Another consequence is that tests of predictive success of models across invaded ranges will tend to generate high omission errors (invaded areas not predicted to be invaded by models) (e.g. Broennimann *et al.* 2007; Fitzpatrick *et al.* 2007) and these may invite potentially erroneous interpretations of shifts in fundamental niches. A pragmatic solution to improve inferences of physiological limits based on geographical distributions of species, is to model species distributions using both native and invaded ranges (Broennimann & Guisan 2008) or, whenever possible, to use historical distributional records (e.g. Nogués-Bravo *et al.* 2008).

Studies in evolution are also bound to be strongly affected by overestimation of niche differences across lineages. Specifically, if the currency of interest is rates of change in physiological aspects of the niche (e.g. Peterson *et al.* 1999; Hof *et al.* 2010; Kozak & Wiens 2010), then overestimation of niche differences among species will lead to inflation of evolutionary rates of the niche and this will lead to erroneous conclusions about niche conservatism and its importance in driving biodiversity patterns on earth.

CONCLUDING REMARKS

The activity of terrestrial animals and plants is limited by their thermal environment. Because environmental temperature varies in time and space, sometimes abruptly, organisms are continually challenged to maintain homeostasis. Here, we asked if physiological adaptation of species to current climate warming was likely, and what the consequences might be if this was not the case. For a large number of terrestrial ectotherms, endotherms and plants, we show that interspecific variation for lower thermal limits is greater than for upper limits. Similar patterns were found among individuals of the same species for a small number of South American lizard species, suggesting that selection could act at intraspecific level for lower thermal tolerances in cold environments, while reduced opportunities might exist for selection of upper tolerances under warm conditions. We also found for a sample of ectotherm and endotherm species that lower limits of tolerance tend to covary with ambient temperature, whereas upper thermal limits tend not to. In other words, natural selection seems to modulate physiological responses to lower temperatures more so than it does to upper temperatures. Two conclusions can be drawn from these results. First, rates of niche evolution vary for different traits. The implication is that controversy regarding rates of niche evolution vs. conservatism cannot be settled unless specific predictions are made and tested for different traits. Although similar statements have been made previously (e.g. Slobodkin & Rapoport 1974), the consequences of this reasoning for the niche conservatism debate have not always been fully appreciated (see for discussion Araújo & Peterson 2012). Second, and more importantly, hard boundaries seem to constrain evolution of upper thermal tolerances beyond given temperature limits. One consequence of strong conservatism of upper thermal limits among terrestrial organisms is that fundamental niches, particularly the upper tails of species-temperature response curves, should be more similar among closely related species than typically inferred with bioclimatic envelope models or with multivariate approaches relating species distributions with environmental predictors (e.g. Hof *et al.* 2010; Kozak & Wiens 2010). Thus, realized niches of species living in cold environments will tend to underestimate upper thermal limits, potentially causing models to overestimate the effects of climate warming on biodiversity (see also Sunday *et al.* 2012). In contrast, realized niches for species in warm environments are closer to their physiological upper thermal limits. In such cases, further climate warming will cause models to predict correctly range contractions, unless species have other means to adapt to increased temperatures.

Improving understanding of the linkages between organisms and environments is critical for understanding rates of the evolution of niches, predicting the effects of climate change on biodiversity, and estimating the risk of invasive species (e.g. Wiens *et al.* 2010). To make progress in this field, greater interaction between otherwise disconnected disciplines is required. Specifically, there is need for greater coordination between empirical and theoretical research programmes that characterize the fundamental niches of species, and these efforts need to feed into the development of models of species geographical distributions that more explicitly account for the physiological mechanisms constraining species distributions (e.g. Buckley *et al.* 2010; Sunday *et al.* 2012; Kearney *et al.* 2013). Only with improved characterization of the physiological constraints on species distributions will researchers be able to quantify the additional contributions of non-climatic factors, such as dispersal and biotic interactions, in shaping ecological niches and geographical distributions.

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William R. Burnside
University of New Mexico, Albuquerque, NM, USA
e-mail: burnsidewr@gmail.com
http://biology.unm.edu/jhbrown/labmembers.shtml

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commentary

Hot research on roasted lizards: warming, evolution and extinction in climate change studies

In volume 328 of Science, a team headed by Barry Sinervo published a study forecasting the effect of increased temperature in lizards. They demonstrate that climate change has already caused extinctions of lizard populations worldwide. They also forecast that if climate change scenarios come true, 40% of all lizard populations and 20% of all species could be committed to extinction by 2080. Predictions are supported by a model that represents how much activity time will be restricted (i.e., hours of restriction; hr) because operative temperatures are too high.

The study uses a multidisciplinary approach incorporating ecophysiology, evolutionary biology, biogeography and phylogenetics. A special strength of the study is that it uses models that are validated with data from recent population extinctions, which is an extremely rare feature in studies assessing climate change effects on biodiversity (but see Araújo et al. 2005). Sinervo et al.'s study links temperature increases to the organismal biology of the lizards making it possible to predict local extinctions. Unfortunately, such a link leads to a worrisome message: "Climate-forced reptile extinctions are happening now" (Huey et al. 2010).

Forecasts of species extinctions due to climate change are typically based on assessments of changes in climatic suitability for species (e.g. Thomas et al. 2004; Thuiller et al. 2005). Sinervo and colleagues go beyond this climate envelope approach and incorporate aspects of the ecology and behavior that are thought to mediate the responses of species to climate change. The incorporation of ecological and behavioral mechanisms into models attempting to provide insight of the likely responses of species to climate change is welcomed (Brook et al. 2009), but when such attempts involve large numbers of species and biogeographical scales compromises between precision and generality are inevitable.

One of such compromises is related to the use of estimated operative temperatures (the equilibrium temperature of a lizard with its thermal environment) in the study. Operative temperatures can vary greatly due to micro-environmental heterogeneity (Bauwens et al., 1996). Lizards may select locations with cooler micro-climates instead of moving higher in altitude or latitude. Open habitat species for example, may encroach into forests (Huey et al. 2009). This study would have benefited from integrating small scale thermal heterogeneity into large scale studies, although precisely how this can be accomplished remains a key challenge for mechanistically motivated models of climate change.

Investigators such as Kearney et al. (2008) and Mitchell et al. (2008) have created biophysical models of the thermal environment of reptiles to make predictions on the effect of global warming on individual species. These models use heat and energy balance equations to relate environmental conditions with ecophysiological traits measured in the laboratory. These relationships can be mapped geographically to evaluate climate suitability for the species of interest. Sinervo et al.

uses a simpler approach: modeling hr as a linear function of maximum temperature. While this approach does not include as much mechanistic detail as a full physical model, like Kearney et al.'s, it is noteworthy for integrating an environmental niche model, ecophysiological traits, and extinction probabilities. This simplification allowed generalizing the model to include a large number of species in their forecast — a feature that would have been unfeasible if more complex mechanistic models were used.

Another breakthrough is their explicit modeling of potential evolutionary change, an aspect that is rarely considered when attempting to forecast the species responses to climate change. The authors relate extinctions with strong selective pressure and argue that a heritability of 0.17 for field active body temperature (Tb) measured for *Sceloporus occidentalis* constrains adaptation. However, heritability is species-, population-, and environment-specific, and when measured in the lab, it might not represent the actual heritability in the field. Methods exist to estimate heritability in the field (Weigensberg and Roff 1996), but they have seldom been used.

Sinervo et al. used a phylogenetic OLS linear regression between Tb and critical thermal maximum (CTmax) to provide evidence that CTmax may not evolve as fast as Tb, and they suggest that increasing Tb would bring the animal dangerously close to CTmax. OLS linear regression assumes that the X variable has no measurement error. In this particular case both traits have measurement error, so RMA (Reduced Major Axis) regression might have been more appropriate (Warton et al. 2006) since it does not assume absence of error in X axis. The slope of RMA regression is always steeper than that of OLS. With a slope of 0.51 for OLS, the RMA slope for the phylogenetic regression might actually be close to 1, inviting the interpretation that, contrary to the conclusions derived from OLS regression, CTmax may evolve as fast as Tb.

In temperate regions, extinctions probabilities correlated better with hr in the spring than in other seasons. Sinervo et al. propose that temperature increases are more evident during the spring and that the spring is more critical than the summer for lizard survival due to either reproductive costs or to a higher need for resources after diapause. However, there are other possible, although non-exclusive reasons that require further scrutiny. Pregnant females, for instance, often have lower Tb resulting in longer hr in springtime (Carretero et al. 2005), and temperature increase may alter egg development (Mitchell et al. 2008).

Methods inevitably reflect the need to compromise precision with generality. Like other biogeographic studies with strong implications for policy, the sensitivity of the conclusions to the assumptions and methods requires systematic scrutiny (Whittaker et al. 2005). Nevertheless, this study is a "tour-de-force" that exemplifies research opportunities for biogeographers and provides evidence that reptiles might be more sensitive to climate warming than previously reported (e.g. Araújo et al. 2006). Firstly, the study illustrates the value of interdisciplinary collaborations. Biogeographers interested in climate change should consider collaborating with evolutionary biologists, geneticists, systematicians, and ecophysiologists. Secondly, the ecophysiological basis for the study helps create a compelling link between climate change and the organismal biology of the lizards. Thirdly, evolutionary changes are modeled in the context of phylogenetic constraints and genetics. All in all, Sinervo et al. has contributed to launching a new pathway for investigation of climate change impacts on biodiversity. Biogeography has always been an interdisciplinary field, but this study suggests that even broader interdisciplinary collaborations are necessary to help understand the effects of climate change on organisms.

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Francisco Ferri-Yáñez
Museo Nacional de Ciencias Naturales (CSIC), Madrid, Spain; and Laboratorio Internacional de Cambio Global, UC-CSIC, Facultad de Ciencias Biológicas, PUC, Santiago, Chile
e-mail: francisco_ferri@mncn.csic.es
http://www.biochange-lab.eu/people/current-members/paco-ferri

Jack P. Hayes
University of Nevada Reno, USA
http://www.unr.edu/biology/hayes.htm

Miguel B. Araújo
Museo Nacional de Ciencias Naturales (CSIC), Madrid, Spain; and Laboratorio Internacional de Cambio Global, UC-CSIC, Facultad de Ciencias Biológicas, PUC, Santiago, Chile
http://www.biochange-lab.eu/people/principal-investigator

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Thermal tolerances in rodents: species that evolved in cold climates exhibit a wider thermoneutral zone

Francisco Bozinovic[1], Francisco Ferri-Yáñez[2,3,4], Hugo Naya[5],
Miguel B. Araújo[2,3,4] and Daniel E. Naya[6]

[1]*Departamento de Ecología and Center of Applied Ecology and Sustainability (CAPES), Facultad de Ciencias Biológicas, Universidad Católica de Chile, Santiago, Chile,* [2]*Departamento de Biogeografía y Cambio Global, LINCGlobal, Museo Nacional de Ciencias Naturales, Madrid, España,* [3]*InBIO-CIBIO, Universidad de Évora, Évora, Portugal,* [4]*Imperial College London, Silwood Park Campus, Ascot, Berkshire, UK,* [5]*Instituto Pasteur de Montevideo and Departamento de Producción Animal y Pasturas, Facultad de Agronomía, Universidad de la República, Montevideo, Uruguay and* [6]*Departamento de Ecología y Evolución, Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay*

ABSTRACT

Background: Thermal constraints are often invoked to explain animal distributions. Maximum temperatures are less variable in different biomes around the globe than are minimum temperatures. Considerable information is available for mammals about basal metabolic rate and thermal conductance.

Aims: Evaluate the correlation of lower critical temperature (T_{LC}), upper critical temperature (T_{UC}) or TNZ breadth ($T_{UC} - T_{LC} = TNZ_b$) with three ambient temperatures in rodent species.

Hypotheses: T_{LC}, T_{UC} and TNZ_b should be adjusted by selective processes to the ambient temperature that is most usually experienced by mammal species. TNZ_b should be greater in species inhabiting colder habitats.

Methods: We used T_{LC}, T_{UC} data from published studies of 85 species of rodents. We determined the average annual mean, minimum and maximum temperatures across the distribution of each species. Then, using standard least squares regression with body mass as a covariate, we determined the statistical relationships between the physiological variables and the temperatures. We evaluated the effect of phylogeny using a Bayesian Phylogenetic Mixed Model in addition to Bayesian Model Averaging.

Results: Ambient temperatures correlate positively with T_{LC} and T_{UC}, and negatively with TNZ_b. Species that evolved in cold climates exhibited a greater mass-independent TNZ_b than species from warmer climates. Species that evolved in cold climates exhibited lower T_{LC} and T_{UC} than species from warmer climates. Phylogenetic as well as conventional statistics indicated that there are thermoregulatory constraints across geographic gradients.

Keywords: macrophysiology, energetics, environmental temperature, global ecology,
climate change, small mammals.

Correspondence: F. Bozinovic. Departamento de Ecología, CAPES & LINCGlobal, Universidad Católica de Chile, Santiago 6513677, Chile. e-mail: fbozinovic@bio.puc.cl

INTRODUCTION

Understanding the factors that determine the geographic range limits of species is essential to address fundamental questions in ecology, biogeography and evolutionary biology and is particularly pressing because of ongoing environmental global change (Pearson and Dawson, 2003; Martin *et al.*, 2013). Macrophysiology has recently emerged from the integration of physiological ecology and macroecology (Chown *et al.*, 2004) to elucidate the contribution of physiological traits to the geographic distributions of organisms. In other words, macrophysiology is a conceptual convergence between the fields of global ecology and physiology in the study of large spatial- and temporal-scale patterns to explain how high levels of environmental variability affect physiological traits.

Over the past decade, many climate-based hypotheses regarding variation in the distribution range of species have emerged (see Pither, 2003), such as the climate variability hypothesis, the climate extreme hypothesis, and the optimal climate hypothesis. These hypotheses use data on physiological traits of the species, focusing mainly on variation in latitude and altitude (Spicer and Gaston, 1999) and using principally the intrinsic physiological properties of species to predict their responses to climatic variables and how these properties may affect the geographic ranges of assemblages, species and populations (Bozinovic *et al.*, 2011; Naya and Bozinovic, 2012).

Environmental temperature exerts an influence on most levels of biological hierarchy, and thermal physiology is one key factor underpinning the ecological and evolutionary success of animals. Thermal conditions vary over space and time, and thus populations and species are continuously challenged to maintain homeostasis. Individuals are expected to evolve physiological adaptations, physiological tolerances and acclimatization to local conditions in different and likely heterogeneous environments along geographic ranges. Accordingly, thermoregulatory and energetic constraints factors often have been invoked to explain animal distributions (Lovegrove, 2000; Rezende *et al.*, 2004). However, few studies have examined the relationship between plasticity of energetic traits, other than oxygen consumption, and the distribution of endotherms (but see Rodriguez-Serrano and Bozinovic, 2009; Araújo *et al.*, 2013; Naya *et al.*, 2013a, 2013b; Khalik *et al.*, 2014). The thermoneutral zone (TNZ) limits provide an index of an endotherm's temperature comfort range. Within the limits of TNZ are the basal metabolic rates, i.e. endotherms do not have to expend large amounts of energy to maintain thermoregulatory homeostasis. At the lower limit of the thermoneutral zone is the T_{LC} (lower critical temperature) and at the upper limit is the T_{UC} (upper critical temperature; see Fig. 1). Recently, Riek and Geiser (2013) provided the first phylogenetic analyses on scaling of T_{LC}, T_{UC} and TNZ in mammal species. Also, they demonstrated that mammalian TNZ breadth (TNZ_{b}) varied from nearly 1°C to as high as 21°C, a range that is not only affected by body mass but also by thermal conductance.

Here we evaluate the correlation between T_{LC}, T_{UC} and TNZ_{b} ($= T_{\mathrm{UC}} - T_{\mathrm{LC}}$) and three different ambient temperatures for 85 rodent species, using a model selection approach to compare the predictive power of different statistical models. We hypothesize that since basal metabolic rate and thermal conductance are both sensitive to climatic variables (Naya *et al.*, 2013b), and these physiological traits are mainly adjusted – in an evolutionary sense – by selective processes to ambient temperature (Bozinovic *et al.*, 2011; Naya *et al.*, 2013a), then T_{LC}, T_{UC} (Araújo *et al.*, 2013) and TNZ_{b} should also be correlated with geographic temperature. In addition, given that minimum temperatures show a much steeper change across the globe

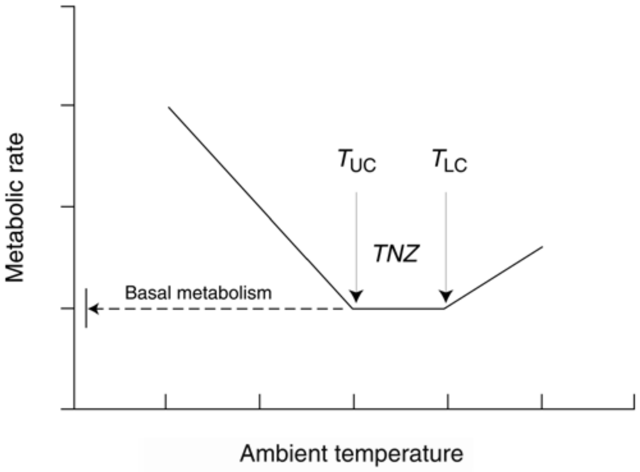

Fig. 1. Fundamental relationships between ambient temperature and metabolic rate for endotherms. The thermoneutral zone (*TNZ*) limits provide an index of an endotherm's temperature comfort range. Within the limits of *TNZ* is basal rate of metabolism. At the lower limit of the thermoneutral zone is the T_{LC} (lower critical temperature) and at the upper limit is the T_{UC} (upper critical temperature).

than maximum temperatures, we expect TNZ_b to be wider in species inhabiting colder habitats (see Araujo *et al.*, 2013).

MATERIALS AND METHODS

Dataset

Data relating to T_{LC}, T_{UC} and the breadth of TNZ_b (calculated as $T_{UC} - T_{LC}$) from published studies on 85 species of rodents from different families and latitudes are available upon request together with data on habitat temperature (T_{med}, mean annual temperature; T_{min}, minimum temperature of coldest month; and T_{max}, maximum temperature of warmest month). A synthetic metric of ambient temperature was calculated as the average temperature across the distribution of a species. Species distributions were obtained from Hijmans *et al.* (2005) and climatic variables were obtained from the WorldClim dataset (Holt *et al.*, 2013) at 2.5 arc minutes resolution. Species distributions and environmental variables were processed using the software Qgis 1.8.0-Lisboa (QGIS Development Team, 2013).

Data analyses

The relationships between thermal variables (T_{LC}, T_{UC} and TNZ_b) and ambient temperatures (T_{med}, T_{min} and T_{max}) were evaluated through standard least squares regression techniques, using body mass as a covariate. We ran single regression models with one ambient temperature (in addition to log body mass), and also multiple regression models with two ambient temperatures (in addition to log body mass). We estimated the goodness of fit of each model and used the Bayesian Information Criterion (BIC) to compare among them. Specifically, a model was selected as a 'good model' if its BIC value did not differ from the overall best model BIC value (which represents, by definition, the lowest BIC value) by more than 2.3 units (Raftery *et al.*, 1997). All these analyses were performed using the R package leaps (Raftery *et al.*, 1997). The effect of phylogeny on the relationship between thermal variables and ambient temperatures was evaluated using a Bayesian Phylogenetic Mixed Model (Bayesian PMM) (Naya *et al.*, 2006; Lumley and Miller, 2009), as well as Bayesian Model Averaging (BMA) (Raftery *et al.*, 1997). A phylogenetic tree was built up by combining the tree published by Lovegrove (2003) with the tree published by Huchon and Douzery (2001) (hystricognath rodents). Species that were not present in any of these trees were included at the best resolution level, according to the family or genus to which they belong. We decided to incorporate phylogenetic uncertainty in the calculations using BMA because: (1) branch lengths are not known for our super-tree, and (2) there are several soft polytomies associated with (1). Consequently, we included phylogenetic uncertainty by generating 1000 trees in which polytomies were randomly resolved (by transforming all multichotomies into a series of dichotomies with one or several branches of length zero), and branch lengths were randomly sampled from a uniform distribution (ranging between 0.01 and the maximum branch length). For each comparative model, the effect of ambient temperatures on thermal variables was calculated through linear mixed models, using body mass as a covariate. Then, to estimate the effect of each ambient temperature on T_{LC}, T_{UC} and TNZ_{b}, we calculated the proportion of posterior estimates larger than zero (gt0). In short, gt0 can be viewed as the probability of observing a positive (if gt0 > 0.5) or negative (if gt0 < 0.5) association between each thermal variable and each ambient temperature. Note that when a thermal variable is unaffected by an ambient temperature, the probability is equal to 0.5 (i.e. the distribution of the regression coefficients is centred on zero). All comparative analyses were performed using the software R, through packages 'APE' (http://cran.r-project.org/web/packages/ape/index.html) and 'bmaMCMCanalysis' (L. Spangenberg *et al.*, submitted, available upon request).

RESULTS

The relationships between thermal variables (in °C) and body mass (m_{b} in g) were highly significant for T_{LC} and TNZ_{b}, but not for T_{UC}. The allometric relationships were described by the following functions:

$$T_{\mathrm{LC}} = 36.03\, m_{\mathrm{b}}^{-0.0687} \tag{1}$$
$$(r = -0.66,\ \mathrm{d.f.} = 83,\ P = 1.0\mathrm{E}^{-11})$$

$$T_{\mathrm{UC}} = 34.48\, m_{\mathrm{b}}^{-0.0072} \tag{2}$$
$$(r = -0.16,\ \mathrm{d.f.} = 83,\ P = 0.16)$$

$$TNZ_{\mathrm{b}} = 2.45\, m_{\mathrm{b}}^{0.1957} \tag{3}$$
$$(r = 0.54,\ \mathrm{d.f.} = 83,\ P = 1.2\mathrm{E}^{-7})$$

Regarding the effect of ambient temperatures, we found that ambient temperatures were positively correlated with T_{LC} and T_{UC} (Tables 1 and 2; Fig. 2a,b) and negatively correlated with TNZ_{b} (Tables 1 and 2; Fig. 3). In addition, based on the BIC values the best models to explain variation in T_{LC} and T_{UC} were those that only included the effect of T_{med} (even though the model that only includes the effect of T_{min} also comprises a 'good model' for T_{UC}), while the best model to explain variation in TNZ_{b} was the one that only included the effect of T_{max} (even though the model that only include the effect of T_{med} also comprises a 'good model' for TNZ_{b}).

Table 1. Results of single- and multiple-factor models with ambient temperature, in addition to body mass

	$\log_{10} m_b$		T_{med}		T_{min}		T_{max}		
	r	P	r	P	r	P	r	P	BIC
T_{LC}	−0.75	$2.3E^{-17}$	0.47	$2.8E^{-9}$	—	—	—	—	405.54
T_{LC}	−0.78	$2.0E^{-16}$	—	—	0.43	$2.2E^{-7}$	—	—	414.36
T_{LC}	−0.64	$7.8E^{-14}$	—	—	—	—	0.41	$1.3E^{-7}$	413.36
T_{LC}	−0.73	$9.1E^{-16}$	0.74	0.002	−0.30	0.21	—	—	408.30
T_{LC}	−0.73	$1.8E^{-15}$	0.36	0.004	—	—	0.12	0.30	408.83
T_{LC}	−0.72	$4.0E^{-15}$	—	—	0.26	0.005	0.25	0.008	410.29
T_{UC}	−0.24	0.02	0.39	0.0003	—	—	—	—	377.91
T_{UC}	−0.27	0.01	—	—	0.40	0.0003	—	—	378.03
T_{UC}	−0.15	0.16	—	—	—	—	0.28	0.008	384.15
T_{UC}	−0.26	0.02	0.22	0.53	0.19	0.59	—	—	382.05
T_{UC}	−0.26	0.02	0.46	0.01	—	—	−0.08	0.66	382.14
T_{UC}	−0.26	0.02	—	—	0.35	0.01	0.07	0.57	382.13
TNZ_b	0.69	$2.2E^{-12}$	−0.27	0.002	—	—	—	—	416.26
TNZ_b	0.69	$8.9E^{-12}$	—	—	−0.22	0.01	—	—	420.15
TNZ_b	0.62	$2.5E^{-11}$	—	—	—	—	−0.28	0.001	415.04
TNZ_b	0.65	$6.7E^{-11}$	−0.69	0.01	0.45	0.10	—	—	417.93
TNZ_b	0.65	$1.2E^{-10}$	−0.11	0.43	—	—	−0.19	0.18	418.82
TNZ_b	0.64	$1.8E^{-10}$	—	—	−0.06	0.58	−0.247	0.02	419.15

Finally, results obtained by phylogenetically informed analyses were similar to those obtained by conventional statistical methods, such that all the correlations that were significant by conventional methods were also significant by phylogenetically informed methods (Table 2).

DISCUSSION

Phylogenetic as well as conventional statistics indicated that there is a clear correlation between physiological variables and ambient temperatures along geographic gradients. Riek and Geiser (2013) suggested that TNZ_b is related to the apparent thermal conductance and it is consequently possible that basal metabolism at different body masses is a function of both the heat exchange within TNZ and that encountered below and above the TNZ to allow thermoregulatory homeostasis. Recently, Khalik *et al.* (2014) studied the global variation in thermal tolerances and vulnerability of birds and mammals to climate change. Surprisingly, these authors found support for the climatic variability hypothesis in birds but not in mammals. According to Khalik *et al.* (2014), species are presently experiencing temperatures within their limits of tolerance, whereas in the future they will be able to tolerate temperatures estimated for different scenarios of global warming. Nevertheless, they highlight tropical regions are highly vulnerable to global warming.

Naya *et al.* (2013a, 2013b) demonstrated that mean and minimum temperatures plus accumulated rainfall were the main predictors of mass-independent variation in basal

Table 2. Parameter estimation (*B*), standard deviation (SD) and proportion of posterior estimates greater than zero (gt0) for single- and multiple-factor models, according to phylogenetically informed analysis

	T_{med}			T_{min}			T_{max}		
	B	SD	gt0	*B*	SD	gt0	*B*	SD	gt0
T_{LC}	0.2146	0.0401	0.9999	—	—	—	—	—	—
T_{LC}	—	—	—	0.1338	0.0292	0.9999	—	—	—
T_{LC}	—	—	—	—	—	—	0.2793	0.0594	0.9999
T_{LC}	0.3436	0.1264	0.9964	−0.0958	0.0891	0.1397	—	—	—
T_{LC}	0.1702	0.0716	0.9907	—	—	—	0.0767	0.1033	0.7731
T_{LC}	—	—	—	0.0781	0.0374	0.9816	0.1761	0.0765	0.9889
T_{UC}	0.1145	0.0335	0.9995	—	—	—	—	—	—
T_{UC}	—	—	—	0.0770	0.0237	0.9994	—	—	—
T_{UC}	—	—	—	—	—	—	0.1183	0.0499	0.9908
T_{UC}	0.1083	0.1073	0.8455	0.0045	0.0757	0.5235	—	—	—
T_{UC}	0.1494	0.0605	0.9930	—	—	—	−0.0604	0.0874	0.2425
T_{UC}	—	—	—	0.0681	0.0312	0.9851	0.0284	0.0641	0.6732
TNZ_b	−0.1043	0.0433	0.0084	—	—	—	—	—	—
TNZ_b	—	—	—	−0.0592	0.0311	0.0291	—	—	—
TNZ_b	—	—	—	—	—	—	−0.1679	0.0618	0.0037
TNZ_b	−0.2479	0.1393	0.0368	0.1065	0.0980	0.8622	—	—	—
TNZ_b	−0.0247	0.0769	0.3716	—	—	—	−0.1384	0.1108	0.1043
TNZ_b	—	—	—	−0.0110	0.0401	0.3899	−0.1528	0.0821	0.0318

Note: Body mass contribution was significant in all cases ($gt0 < 0.05$).

metabolism. These authors also reported a significant and positive relationship between mass-independent thermal conductance and mean annual temperature plus accumulated rainfall/aridity (or aridity), concluding that the same exogenous factors are affecting the evolution of both thermal conductance and metabolic rate among rodent species (Naya *et al.*, 2013a, 2013b). Indeed, in the present study we found that temperatures were positively correlated with T_{LC} and T_{UC}, and negatively correlated with TNZ_b. Therefore, species that evolved in cold climates exhibited lower mass-independent T_{LC} and T_{UC} than species from warmer habitats. Also, rodents that evolved in cold climates exhibited a wider mass-independent TNZ_b than species from warmer habitats

There may be two not completely exclusive (statistical) reasons why TNZ_b is negatively correlated with ambient temperature while T_{LC} and T_{UC} are positively correlated with temperature. One possibility is that high environmental temperatures are less variable than cold temperatures (Addo-Bediako *et al.*, 2000; Boher *et al.*, 2010), so that perfect tracking of T_{UC} to high temperature would imply less variation than perfect tracking of T_{LC} to low temperatures. The second possibility is that it is more difficult to increase T_{UC} because of a high probability of a destabilizing effect of high temperature on cell membranes and protein structure and function than to decrease T_{LC}, and thus, although both correlate with ambient temperature, T_{LC} would be more strongly correlated (higher slope) with ambient temperature than T_{UC}. Although a higher geographical variation of minimum temperatures

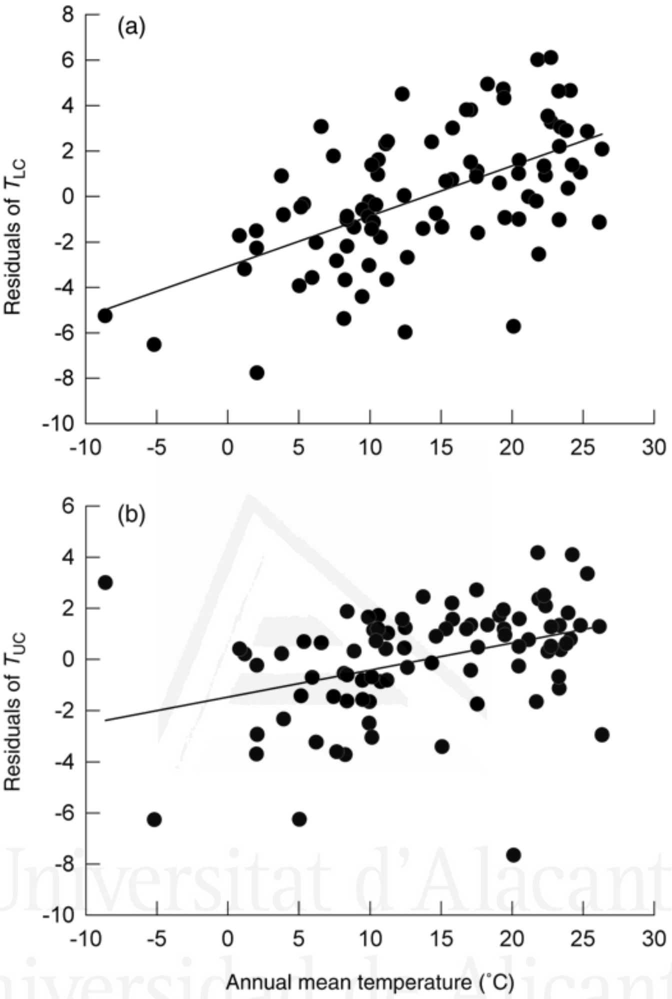

Fig. 2. Relationship between (a) residuals of lower critical temperature, T_{LC} (with regard to body mass) and (b) residuals of upper critical temperature, T_{UC} (with regard to body mass) and mean annual temperature.

than maximum temperatures has been reported (Sunday *et al.*, 2013), the results of the phylogenetically informed analysis in Table 2 show that the correlations between T_{LC} and environmental temperature are always higher than those between T_{UC} and environmental temperature, which provides support for the second hypothesis and is in line with the pattern recently reported for several taxa (Araújo *et al.*, 2013). In other words, the heat tolerance of rodents is more conserved with little variation by latitude and environmental temperature, but cold tolerance decreases significantly with environmental temperature and latitude and exhibits marked variability.

Araújo *et al.* (2013) asked if species adapt physiologically to climate warming. These authors analysed thermal tolerances of a large number of terrestrial ectotherms, endotherms and plant species across the world, and found that tolerance to heat is largely

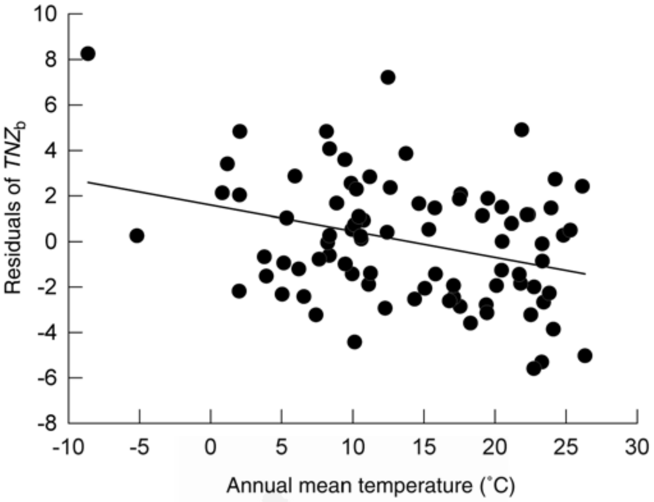

Fig. 3. Relationship between residuals of the breadth of the thermoneutral zone, TNZ_b (with regard to body mass) and mean annual temperature.

conserved across lineages, but tolerance to cold varies between and within species. This pattern challenges the classic view that physiological tolerances of species change continuously across climatic gradients, and portrays an alternative view in which the thermal component of climatic niches would overlap across species more than expected. One consequence of this conservatism of upper tolerances is that the upper thermal limits for cold-adapted species will likely be underestimated, so potentially inflating assessments of risk from climate change. In contrast, species whose climatic preferences are close to their upper thermal limits are unlikely to evolve physiological tolerances to increased heat, and could predictably be more affected by global warming.

Finally, our study provides good evidence that long-term average temperatures could affect small mammals' – in our case rodent species' – thermoregulatory capabilities on an evolutionary scale. However, it is important to note that energetic traits can change among populations within each species and also within a single individual throughout its life [developmental plasticity, seasonal flexibility (e.g. Johnston and Bennett, 1996; McKechnie, 2008)]. Thus, a basic assumption of our study is that intraspecific variation in energetic traits is of a lower magnitude than interspecific variation. Unfortunately, at the present time, there are not enough data to empirically test this assumption, but data on basal metabolic rates suggest that this is indeed the case (Naya *et al.*, 2013a). In addition, the fact that we were able to detect a clear pattern of variation even though we did not control for several sources of intraspecific variation (e.g. we used environmental data averaged throughout a species' distributional range and not for each specific site of collection) indicate that the reported global trend is a strong one. Further work is needed to estimate the relative importance of different source of intra-specific variation in *TNZ* in small endotherms. A second restriction arises from the character of the study itself. Indeed, comparative studies must trade off precision for generality, and ours is no exception. The use of coarse meteorological variables, for instance, may not accurately reflect those microclimates that species are really experiencing in the field as well as the whole geographic range of each species. The significant relationships between T_{LC}, T_{UC}, and TNZ_b and temperature obtained with such a conservative approach suggests, however, that behavioural traits cannot totally compensate differences in thermal environments estimated with weather station data. On the other hand, our taxonomic database is just a small sample of the vast diversity of rodent species. Future studies should not only assess the generality of our results, but also the mechanistic basis that could account for these patterns as well as a large database of species and habitat diversity.

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Nota

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Liolaemus flavipiceus Cei & Videla, 2003: primer registro en Chile y nuevos antecedentes para el taxón (Reptilia, Sauria, Liolaemidae)

Carlos F. Garin A.[1], Jaime Troncoso-Palacios[2], Francisco Ferri Y.[3,4], Gabriel Lobos V.[5]

[1] Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Santiago, Chile.

[2] Programa de Fisiología y Biofísica, Facultad de Medicina, Universidad de Chile, Santiago, Chile.

[3] Dpto. Biogeografía y Cambio Global, Museo Nacional de Ciencias Naturales, CSIC, Madrid, España.

[4] Laboratorio Internacional en Cambio Global, CSIC-PUC, Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Santiago, Chile.

[5] Centro de Estudios de Vida Silvestre (CEVIS), Facultad de Ciencias Veterinarias y Pecuarias, Universidad de Chile, Santiago, Chile.

Con más de 230 especies descritas, *Liolaemus* constituye uno de los géneros de amniotas más diversos del planeta (Lobo *et al.*, 2010; Uetz, 2012). Taxón exclusivo del cono sur de Sudamérica, distribuido principalmente en Argentina y Chile (Pincheira-Donoso *et al.*, 2008), su taxonomía y sistemática se encuentra en un momento de gran dinamismo, lo que no ha estado exento de controversias (Lobo *et al.*, 2010; Pincheira-Donoso, 2011). Ejemplo de esto es la alta tasa de descripción de nuevos taxa en los últimos años: sólo durante el primer semestre de 2012 se han señalado ocho nuevas especies para Argentina (Abdala *et al.*, 2012a,b; Avila *et al.*, 2012; Quinteros, 2012). En Chile, además de las nuevas descripciones, el descubrimiento de taxa ya descritos en países limítrofes ha contribuido de manera importante en dilucidar la estructura taxonómica de los reptiles chilenos (Donoso-Barros y Codoceo, 1962; Núñez y Torres-Mura, 1992; Pincheira-Donoso y Núñez, 2005). Colectas herpetológicas efectuadas en la cordillera andina de la VII Región de Chile, específicamente en los alrededores del embalse artificial conocido como Laguna del Maule, cerca de 16 km del límite internacional con Argentina, dieron como resultado el hallazgo de individuos de una nueva especie para el país, *Liolaemus flavipiceus* Cei y Videla, 2003, taxón perteneciente al complejo *elongatus-kriegi* y al clado *punmahuida* (Avila *et al.*, 2010) y hasta ahora descrito exclusivamente para la cuenca superior del Río Pehuenche, cercanías del Paso Internacional Pehuenche, 2500 m, Departamento de Malargüe, Provincia de Mendoza, Argentina (Cei y Videla, 2003), y previamente considerados como *Liolaemus kriegi* (Mella, 2005). El objetivo del presente trabajo es adicionar a *L. flavipiceus* a la herpetofauna chilena y entregar nuevos antecedentes en orden de complementar la diagnosis original de esta especie.

Se analizó una muestra de 16 ejemplares provenientes de los alrededores del embalse Laguna del Maule, Comuna de San Clemente, Provincia de Talca, VII Región del Maule, aproximadamente 2150 m (36°00'42,8"S; 70°33'24,2"W; Datum WGS84, Fig. 1). Nueve individuos (dos machos y siete hembras) fueron capturados a principios de marzo de 2008 en zonas rocosas adyacentes a la laguna, aguas abajo del pretil del embalse. Esta muestra se complementó con dos individuos (un macho y una hembra), obtenidos en febrero de 2012 aguas arriba del pretil. El diseño y color en vida fueron registrados mediante fotografía digital. Los ejemplares fueron sacrificados por inyección intraperitoneal de lidocaína al 1% (Solin®),

Figura 1. Distribución de *Liolaemus flavipiceus* en Argentina y Chile. Círculo negro: Paso Pehuenche (localidad tipo). Cuadrado negro: Laguna del Maule.

Autor para correspondencia: cgarin@bio.puc.cl fijados con alcohol al 95%, preservados en alcohol al 70% e ingresados a la Colección Herpetológica del Museo Nacional de Historia Natural, Santiago de Chile (MNHNCL) y a la Colección de Flora y Fauna Prof. Patricio Sánchez Reyes del Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica, Santiago de Chile (SSUC Re). El sexado de los ejemplares se realizó a través de la observación de gónadas *in situ*. Conjuntamente se revisaron cinco individuos (tres machos y dos hembras) provenientes de la misma localidad y depositados en la Colección Herpetológica del MNHNCL sin asignación específica (ver material examinado en Apéndice). Las medidas fueron tomadas mediante vernier digital (0,1 mm de precisión). La obtención de valores morfométricos y merísticos siguen, en general, los criterios y procedimientos indicados en la literatura (Etheridge, 1995; Lobo, 2001, 2005; Pincheira-Donoso y Núñez, 2005). Todos los antecedentes de *L. flavipiceus* fueron obtenidos a partir de la publicación original de la especie (Cei y Videla, 2003).

Según Cei y Videla (2003), las principales características diagnósticas de *L. flavipiceus* son la carencia de poros precloacales en ambos sexos y el número relativamente alto de escamas en el medio del cuerpo, las que son suavemente quilladas en la zona dorsal, exceptuando las de la región vertebral, más gruesas y con quillas más marcadas. Presentaría además un notorio patrón dorsal, constituido por una amplia banda lateral de escamas negras con predominio medial de escamas amarillas, las que aumentan hacia posterior alcanzando hasta la base de la cola. Ninguno de nuestros ejemplares presentan poros precloacales. Por otro lado, todos los valores morfométricos se encuentran dentro del intervalo de los de la descripción original de las cercanías del Paso Pehuenche (Tabla 1). Sin embargo, Cei y Videla (2003) destacan la existencia de dimorfismo sexual en la longitud hocico-cloaca, siendo los machos notoriamente más grandes (n = 5; $\overline{X}$ = 90,3 mm; intervalo = 86,5 – 95,0 mm) que las hembras (n = 5; $\overline{X}$ = 80,3 mm; intervalo = 77,0 - 84,2), sin superposición en los intervalos. Los individuos de Laguna del Maule no evidencian diferencias significativas en el tamaño (ts = -0,119; g.l. = 14; p = 0,9) entre machos (n = 6; $\overline{X}$ = 82,7; intervalo = 68,6 – 94,9) y hembras (n = 10; $\overline{X}$ = 82,1; intervalo = 70,2 – 95,6). El mayor número de hembras utilizadas en este trabajo, muchas de gran desarrollo corporal, eventualmente explicarían estas diferencias. En cuanto al número de escamas alrededor del medio del cuerpo, no se observa correspondencia entre ambas localidades (mayor número en Paso Pehuenche, sin superposición de intervalos, Tabla 1). Sin embargo, Cei y Videla (2003) sólo indican el valor obtenido en el holotipo de *L. flavipiceus*, sin mencionar la variación a partir de los paratipos, señalando explícitamente que: *"Dorsal scale rows are very irregular in this species, greatly difficulting a clear calculation of its very high scale number at midbody"* (p. 280). Concordamos con Cei y Videla (2003) en esto último, por lo que nuestra diferencia de cinco escamas entre nuestro mayor valor y el holotipo de *L. flavipiceus* no constituye argumento en contra de la correspondencia taxonómicas entre ambas poblaciones.

Un carácter quizás sobreutilizado en las diagnosis de *Liolaemus*, lo constituye el patrón de diseño y coloración, particularmente en la diferenciación de taxa carentes de poros precloacales y de similar morfometría, lepidosis y ecología, tales como *L. tregenzai* y *L. punmahuida* (Avila *et al.*, 2003; Pincheira-Donoso y Scolaro, 2007;). Cei y Videla (2003) señalan como una de las principales características de *L. flavipiceus* su coloración dorsal peculiar, la que determina su nombre específico (del latin *flavus*, amarillo, y *piceus*, negruzco). Esta se compone de bandas laterales de escamas negras con predominio medial de escamas amarillas, las que van aumentando hacia la parte posterior del dorso hasta llegar a ser predominantes en la base de la cola (ver Plate 1:1 en Cei y Videla 2003). Ventralmente la coloración sería oscura o rojiza, con densas manchas negruzcas en la garganta y pecho. Un individuo fotografiado en Laguna del Maule se corresponde perfectamente con esta descripción (Fig. 2). Cei y Videla (2003) indican además diferencias sexuales en la coloración dorsal y ventral, en donde los machos presentarían un patrón dorsal más uniforme y oscuro que las hembras, con prevalencia de escamas amarillas, naranjas o rojizas. De igual forma, la tendencia a una coloración ventral oscura (negruzca o rojiza) sería más acentuada en los machos que en hembras, las que mostrarían tonalidades blanquecinas o azuladas con numerosas escamas naranjas. Sin embargo, los ejemplares de Laguna del Maule no evidencian el dicromatismo sexual destacado por Cei y Videla (2003), sino más bien una marcada variabilidad de coloración y patrón de diseño en ambos sexos (Fig. 3), con hembras con las características indicadas para los machos del Paso Pehuenche, tales como patrón dorsal oscuro y uniforme con escamas amarillas (Fig. 3A, 3B, 3C)

Tabla 1. Promedio (Intervalo) de los caracteres morfométricos y merísticos de *L. flavipiceus* provenientes de las cercanías del Paso Pehuenche y Laguna del Maule. LHC = longitud hocico-cloaca; LC = longitud de la cola; LEA = longitud de la extremidad anterior; LEP = longitud de la extremidad posterior; LAI = distancia axila-ingle; Lcab = longitud de la cabeza; Acab = ancho de la cabeza; Lhoc = longitud del hocico; EMC = número de escamas alrededor del medio del cuerpo. Las medidas están expresadas en milímetros. Los datos del Paso Pehuenche fueron obtenidos de Cei y Videla (2003), en donde se entrega Lhoc y EMC sólo del holotipo.

L. flavipiceus	LHC	LC	LEA	LEP	LAI	Lcab	Acab	Lhoc	EMC
Paso Pehuenche (n = 10)	85,3 (77-95)	113,8 (104-124)	31,8 (28,5-35,2)	48 (44,2-53)	40,7 (34,2-46)	17,6 (16,2-19,2)	15,7 (14-18,2)	5,7	83
Laguna del Maule (n = 16)	82,3 (68,6-95,6)	112,3 (102,9-123)	31,8 (27,6-37,9)	46,8 (38,8-53,5)	40,4 (30-51,5)	17,4 (15,4-21,3)	15 (11,4-17,4)	5,5 (4,2-6,8)	71,9 (68-78)

o ventral oscuro rojizo (Fig. 3E). Esta situación constituye un llamado a la cautela en la utilización de este tipo de caracteres, que pueden ser altamente variables y resultar insuficientes para las diagnosis de nuevos taxa de *Liolaemus*.

Esta nueva población de *Liolaemus flavipiceus* fue registrada sólo en los alrededores de la Laguna del Maule, a partir de los 2150 m aproximadamente. Se trata de una zona volcánica con vegetación rala y abundantes rocas basálticas. Los individuos se observaron sobre rocas cercanas a cursos de agua, ocultándose en cuevas bajo éstas. Las especies de reptiles sintópicos los constituyen, en orden de abundancia, *Liolaemus* sp., *Phymaturus maulense* Núñez, Veloso, Espejo, Veloso, Cortés y Araya, 2010, y *L. buergeri* Werner, 1907. Aguas abajo del embalse, siguiendo el curso del Río Maule, *L. flavipiceus* desaparece, manteniéndose las otras especies de lagartijas, las que aumentan su abundancia (particularmente *Liolaemus* sp. y *Phymaturus maulense*). Bajo los 1500 m, los taxa altoandinos son reemplazados por *L. schroederi* Müller y Hellmich, 1938, *L. lemniscatus* Gravenhorst, 1838, y *L. chiliensis* (Lesson, 1828).

Por último, estos hallazgos permiten descartar la presencia de *Liolaemus kriegi* Müller y Hellmich, 1939, en Laguna del Maule, mencionado anteriormente para esta localidad por Mella (2005), sin indicar especímenes examinados. A la luz de nuestros resultados, esta población correspondería claramente a *L. flavipiceus*, el que se diferencia de *L. kriegi* por evidenciar los machos de este último cuatro poros precloacales, además de otros caracteres (Cei, 1986).

Figura 2. Ejemplar de *Liolaemus flavipiceus* proveniente de Laguna del Maule, Chile. Fotografía de Yamil Hussein E.

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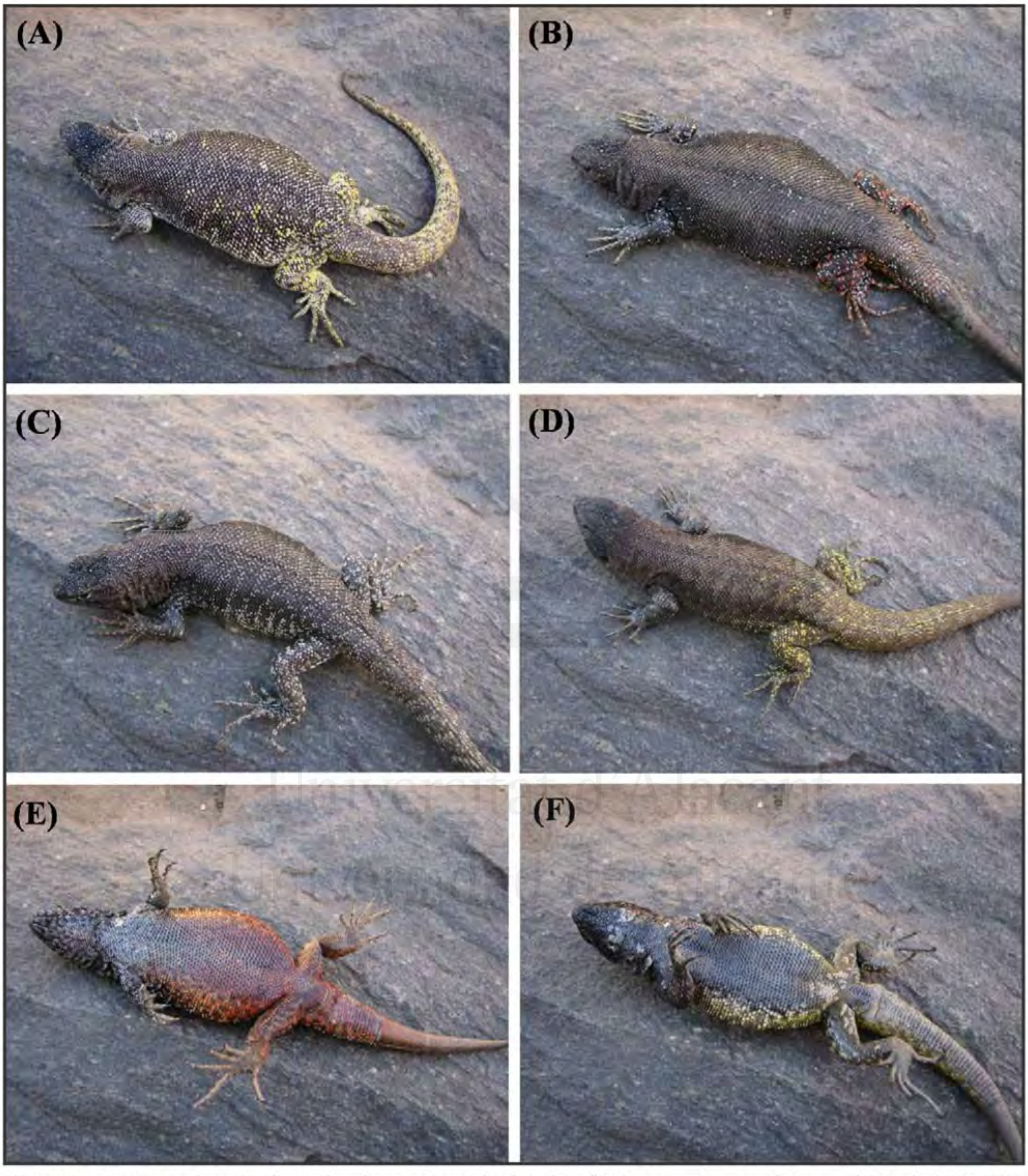

Figura 3. Variación en coloración, diseño dorsal y ventral en individuos de *L. flavipiceus* provenientes de Laguna del Maule. (A) Hembra MNHNCL 4399; (B) Hembra MNHNCL 4402; (C) Hembra MNHNCL 4405; (D) Macho MNHNCL 4407; (E) Hembra MNHNCL 4402; (F) Macho MNHNCL 4407.

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Apéndice

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NOTES ON GEOGRAPHIC DISTRIBUTION

Liolaemus patriciaiturrae Navarro and Núñez, 1993 (Squamata: Liolaemidae): Distribution extension in northern Chile and geographic distribution map

Jaime Troncoso-Palacios [1*] and Francisco Ferri-Yáñez [2,3]

1 Universidad de Chile, Facultad de Medicina, Programa de Biofísica y Fisiología. Casilla 70005. Santiago, Chile.
2 CSIC, Museo Nacional de Ciencias Naturales, Departamento de Biodiversidad y Biología Evolutiva. Calle José Gutiérrez Abascal, 2, 28006, Madrid, Spain.
3 UC-CSIC, Laboratorio Internacional en Cambio Global, Depto de Ecología, Facultad de Ciencias Biológicas, Alameda 340, Santiago, Chile.
* Corresponding author: E-mail: *jtroncosopalacios@gmail.com*

ABSTRACT: We report two new records for *Liolaemus patriciaiturrae* in Chile, one corresponding to specimens previously misidentified as *L. nigriceps*. We also provide a map showing all the known locations of the species.

The genus *Liolaemus* comprises more than 230 species (Abdala *et al.* 2012) distributed from Perú and southern Brazil to Tierra del Fuego. The genus is divided into two subgenera: *Liolaemus* (*sensu stricto*) and *Eulaemus* (Laurent 1983), each of which has been divided into several groups.

Liolaemus patriciaiturrae (Navarro and Núñez 1993) belongs to the *Eulaemus* subgenus, *montanus* section and *montanus* series (Lobo *et al.* 2010). It is a large *Liolaemus* species, with maximum SVL of 96.6 mm. The dorsal color is gray. The throat and chest are black in males. (Navarro and Núñez 1993). This species is not included in the IUCN Red List of Threatened Species (IUCN 2010).

Liolaemus patriciaiturrae was described from El Cerrito, (26°27′ S, 69°03′ W, 3556 m), 12 km NW of La Ola, Atacama, Chile. Later, Moreno *et al.* (2001) mentioned one specimen captured at Nevado Jotabeche (27°40′33″ S, 69°18′08″ W estimated using Google Earth, Figure 1). The species has been recorded from other locations in Atacama, although with no collection of specimens: Laguna Santa Rosa (27°05′23″ S, 69°10′34″ W, estimated using Google Earth) (Moreno *et al.* 2000) and Mina El Hueso, near Potrerillos (26°27′01″ S, 69°28′43″ W, estimated using Google Earth) (Pincheira-Donoso and Núñez 2005).

During a field trip to Atacama in November 2011, we collected two specimens of *L. patriciaiturrae* in Cuesta Montandón (26°23′08″ S, 69°21′34″ W, 3088 m, 16 km W of El Cerrito). The specimens were found among rocks or near bushes, between 11:00 and 15:00 h. The specimens were collected under permit number N°1637 issued by Servicio Agrícola y Ganadero (SAG) and deposited in Colección de Flora y Fauna, Profesor Patricio Sánchez Reyes of Pontificia Universidad Católica de Chile (SSUC Re 163-64, Figures 2 and 3). All specimens were photographed. Midbody scales were counted according to Smith (1946). Ventrals were counted from mental scale to the anterior margin of cloacal opening. Body measurements were taken with a digital vernier (0.02 mm precision). Scale observations were made using magnifying lenses. The characteristics of these specimens matches the original description. We also examined two topotypes; SSUC Re 161-62 from El Cerrito and ten specimens of *L. rosenmanni* from La Ola (Núñez and Navarro 1992) (SSUC Re 142-51, four adults and six juveniles), the only species of the *montanus* series known to be sympatric with *L. patriciaiturrae*.

Additionally, we examined five specimens from Aldebarán (27°27′02″ S, 69°21′57″ W, estimated using

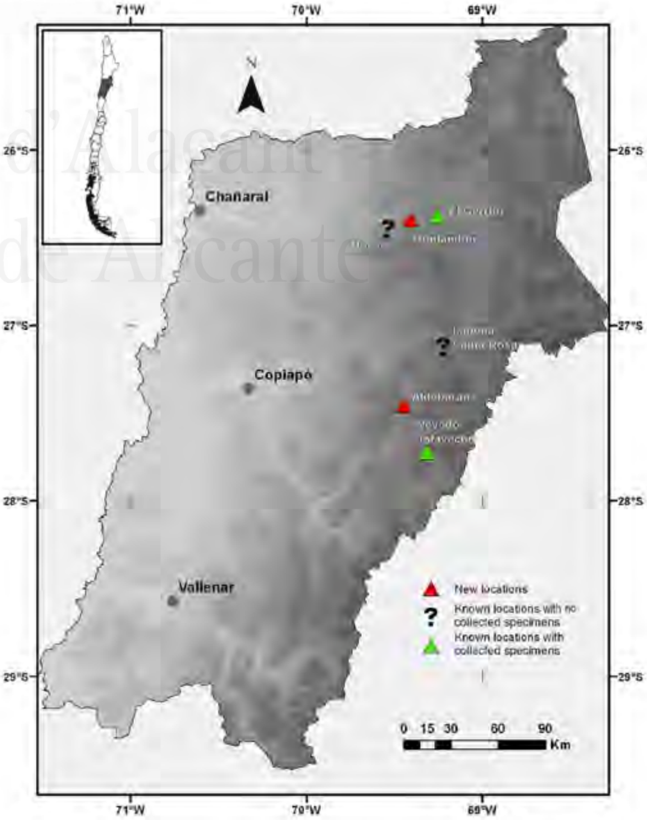

FIGURE 1. Map of Atacama region showing records of *Liolaemus patriciaiturrae*. Green triangles show previous confirmed records, red triangles show the new records and question marks indicate records with no collected specimens. Darker background indicates greater elevation. Upper left: map of Chile showing Atacama region (dark gray).

FIGURE 2. Specimens of *Liolaemus patriciaiturrae*. Topotypes on the left (SSUC Re 161-62). New records from Montandón on the right (SSUC Re 163-64).

FIGURE 3. SSUC Re 164, *Liolaemus patriciaiturrae* from Montandón, new record.

Google Earth, 110 km S of El Cerrito), Río La Gallina, Atacama. These specimens (MNHN-CL 2821-25, Figure 4) were previously identified as *L. nigriceps* (Philippi 1860) by Pincheira-Donoso and Núñez (2005). This led to other authors listing this species as present in Atacama (Troncoso-Palacios and Marambio 2011; Valladares 2011). However, *L. nigriceps* occurs in Pajonales, Llullaillaco (Antofagasta, Chile) and Socompa (Argentina) (Pincheira-Donoso and Núñez 2005) more than 240 km north of Aldebarán. The misidentification probably occurred because the two species are very similar and unfortunately the variation in scale counts and color pattern in *L. patriciaiturrae* were not included in the description of the species (Navarro and Núñez 1993). Our review of eight specimens shows that *L. patriciaiturrae* has gray dorsal background color, with black transverse lines alternating with narrow yellow or white lines, whereas *L. nigriceps* has gray background color with black transverse bars alternating with broad yellow or orange bands (based on four specimens from Llullaillaco, MNHN-CL 2971-73, 2975, Figure 4). On the other hand, *L. rosenmanni* has brown dorsal background color, with bands formed by dark brown and whitish spots, accompanied by yellow or orange spots (Figure 5).

Navarro and Núñez (1993) proposed a diagnosis for *L. patriciaiturrae* based on three characters: large size, gray dorsal color and black throat and chest in males. However, these characters are also present in *L. nigriceps* and the throat is black in both sexes in *L. patriciaiturrae*. Table 1 summarizes some comparative characters among *L. patriciaiturrae*, *L. nigriceps* and *L. rosenmanni*. According to Pincheira-Donoso and Núñez (2005) *L. patriciaiturrae* has 4–5 supraocular scales and *L. nigriceps* has 5–7. However, our data (Table 1) show that this is not a diagnostic character.

On the other hand, the *Liolaemus* from Laguna del Negro Francisco (Figure 5), 25 km from Aldebarán, identified as *L. eleodori* (Cei *et al.* 1985) by Núñez and Torres-Mura (1992) and as *Liolaemus sp.* by Moreno *et al.* (2000), strongly resembles *L. rosenmanni*. Aldebarán is located 80 km S of Pastos Largos, the type locality of *L. rosenmanni*. According to Carlos Garin (personal communication) this population corresponds to *L. rosenmanni*, but a formal study is needed to clarify this issue.

The new records of *L. patriciaiturrae* extend the species' range by 16 km (Montandón) and 110 km (Aldebarán). Although these distances are not large, the new records contribute to the understanding of the habitat and distribution of these rare lizards. Currently, the only elevational data for *L. patriciaiturrae* (3556 m) is provided

FIGURE 4. Top, MNHN-CL 2971-73, 2975, *Liolaemus nigriceps* from Llullaillaco. Bottom, MNHN-CL 2821-25, *Liolaemus patriciaiturrae* from Aldebarán, previously misidentified as *Liolaemus nigriceps*.

in the description (Navarro and Núñez 1993). Therefore the new record from Montandón (3088 m) represents the lowest reported elevation. The only protected population of *L. patriciaiturrae* is in Laguna Santa Rosa (in Parque Nacional Nevado de Tres Cruces). In all other locations the species is threatened by mining projects. The great diversity and similarity among *Liolaemus* species often makes identification difficult. We hope that this contribution will help to distinguish among the members of the *montanus* series.

FIGURE 5. *Liolaemus rosenmanni* from Laguna del Negro Francisco (photograph by Y. Marambio).

TABLE 1. Comparative characters in adults of *Liolaemus patriciaiturrae*, *L. nigriceps* and *L. rosenmanni*.

	L. nigriceps (♂=1, ♀=3)	***L. patriciaiturrae*** (♂=4, ♀=4)	***L. rosenmanni*** (♂=1, ♀=3)
Midbody scales	96–104	90–96	86–92
Ventrals	108–116	90–106	90–100
Supraoculars	5–7	4–7	5–6
Head coloration	Black	Gray to incomplete melanism	Brown with black spots
Throat pattern	Black	Black	Gray with spots (females) / inmaculate dark gray (male)
Precloacal pores (males)	6	6	6
Range of SVL (mm)	84.0–90.3	61.1–91.1	62.3–75.6

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REVISIÓN DEL ESTATUS TAXONÓMICO DE LIOLAEMUS JOSEPHORUM

Núñez, Schulte & Garin 2001 (Iguania: Liolaemidae)

Jaime Troncoso-Palacios[181]
Francisco Ferri-Yánez[182]

Resumen

Se discute la situación taxonómica de *Liolaemus josephorum*, especie que fue propuesta recientemente como un sinónimo junior de *Liolaemus velosoi* sin discutir los caracteres de diagnóstico entre ambos. Su incierta situación taxonómica ha hecho que diferentes autores la consideren una especie valida, pero cuyo estatus taxonómico debe ser revisado. Nosotros examinamos cada uno de estos caracteres de diagnóstico propuestos en la descripción y concordamos con que *L. josephorum* debe ser considerado un sinónimo junior de *L. velosoi*.

Introducción

Liolaemus josephorum Núñez, Schulte & Garin 2001, es una especie descrita para los alrededores de Diego de Almagro (localidad tipo), Finca de Chañaral y El Salvador, en la Provincia de Chañaral, Región de Atacama.

L. josephorum es muy similar a *L. platei* (Werner, 1898) y a *L. velosoi* (Ortiz, 1987), especies que también presentan la escama nasal en contacto con la rostral, ausencia de peine palpebral, heteronotos en los flancos, mancha antehumeral presente o ausente (siempre presente en las otras especies del grupo *nigromaculatus*) y hábitos saxícolas. En su descripción, Núñez *et al.* (2001) usaron caracteres moleculares (DNA mitocodrial), de escamación y de diseño de coloración para diferenciarlo respecto de *L. platei*. Por otra parte, la diagnosis respecto de *L. velosoi* fue realizada basándose en caracteres de escamación y diseño de coloración, sin recurrir a análisis moleculares.

En una reciente revisión de las especies chilenas del genero *Liolaemus*, Pincheira-Donoso & Núñez (2005) consideraron a *L. josephorum* un sinónimo junior de *L. velosoi*: "la recientemente descrita especie propia de Diego de Almagro, *L. josephorum* (Núñez *et*

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[181] Laboratorio de Fisiología y Biofísica, Facultad de Medicina de la Universidad de Chile, Casilla 70005, Santiago de Chile, jtroncosopalacios@gmail.com.

[182] Departamento de Biogeografía y Cambio Global, Museo Nacional de Ciencias Naturales CSIC, Calle José Gutiérrez Abascal 2, 28002, Madrid España. Laboratorio Internacional en cambio Global CSIC-PUC, Depto. de Ecología, Facultad de Ciencias Biológicas, Universidad Católica de Chile, Santiago 6513677, Chile.

al. 2001) no muestra diferencias con *L. velosoi*, de manera que se incluye en su sinonimia" (p. 422). Sin embargo, en Pincheira-Donoso & Núñez (2005) no se discutieron los caracteres de diagnóstico propuestos por Núñez *et al.* (2001) para distinguir a *L. josephorum* de *L. velosoi*.

Pincheira-Donoso & Núñez (2005) revisaron la serie tipo de ambas especies, y uno de los autores (H. Núñez) fue descriptor de *L. josephorum*. Sin embargo, debido a la falta de discusión de los caracteres de diagnóstico, Lobo *et al.* (2010) no aceptan esta sinonimia ("*no supporting data presented*" p. 8).

Posteriormente, Etheridge & Frost (2010) reconocen a *L. josephorum* como una especie válida. La especie también es reconocida como válida por Troncoso-Palacios & Marambio (2011), y Valladares (2011); aunque estos autores indican que es necesario llevar a cabo un estudio para esclarecer su relación con *L. velosoi*.

En este trabajo se revisa la situación taxonómica de *L. josephorum* y se discuten todos los caracteres diagnóstico establecidos por Núñez *et al.* (2001).

Materiales y métodos

Se examinaron nueve topotipos de *L. josephorum* (adultos, 8 machos y una hembra), capturados en la localidad de Diego de Almagro. No fue posible examinar la serie tipo de *L. josephorum* debido a que cuando se escribió este artículo el Museo Nacional de Historia Natural se encontraba cerrado. Se examinaron doce especímenes de *L. velosoi* (adultos, seis machos y seis hembras) recolectados en Estación Paipote y Copiapó, todos determinados como *L. velosoi* por el descriptor de la especie (J.C. Ortiz). No fue posible encontrar los especímenes de la serie tipo de *L. velosoi* que se encuentran depositados en el Museo de Zoología de la Universidad de Concepción al momento de nuestra visita (MZUC 10897-926). Se realizó una comparación de cada uno de los caracteres de escamación mencionados por Núñez *et al.* (2001) como caracteres de diagnóstico entre *L. josephorum* y *L. velosoi*. La observación de las escamas fue hecha bajo lupas de diferente aumento. Para la comparación de los caracteres de coloración, los especímenes fueron fotografiados desde diferentes ángulos. Las medidas del cuerpo (LS = longitud estandar) fueron tomadas con un vernier digital (0,02 mm precisión). Se aplicó la prueba ***exacta*** de ***Fisher*** para comparar las proporciones de presencia de los caracteres examinados, tomando como referencia la proporción de especímenes de *L. josephorum* y *L. velosoi* que presentaron el carácter diagnóstico de *L. velosoi* de acuerdo a Núñez *et al*. (2001). El material estudiado es listado en el Apéndice I.

Resultados

Núñez *et al*. (2001) establecieron un carácter merístico, seis caracteres cualitativos de escamación y cuatro caracteres de coloración como diagnosis entre *L. josephorum* y *L. velosoi.* A continuación se comentan los resultados obtenidos para cada uno de los caracteres:

1) Escudetes impares sobre el hocico (uno en *L. josephorum* y dos en *L. velosoi*, según Núñez *et al*. 2001): El número de escudetes impares sobre el hocico varió entre 2 (44,4%) y 1 (55,6%) en *L. josephorum*, y entre 2 (66,7%) y 1 (33,3%) en *L. velosoi*. No se encontraron diferencias significativas (*P* = 0,396).

2) Forma del interparietal (pentagonal en *L. josephorum* y hexagonal en *L. velosoi*, según Núñez *et al*. 2001): La forma de la escama interparietal variar en ambas especies, siendo hexagonal en la mayor parte de los individuos. En *L. josephorum* fue hexagonal en el 55,6% de los especímenes (pentagonal 22,2%, heptagonal 11,1% y octagonal 11,1%). En *L. velosoi* fue hexagonal en el 66,7% (heptagonal 16,7%, octagonal 8,3% y decagonal 8,3%). No se encontraron diferencias significativas (*P* = 0,673).

3) Forma y disposición de las escamas supratemporales (redondeadas e imbricadas en *L. josephorum* y polimorfitas y yuxtapuestas en *L. velosoi*, según Núñez *et al*. 2001): No se encontraron diferencias cualitativas. Las escamas supratemporales de *L. josephorum* (Fig 1.a) y *L. velosoi* (Fig1.b) son polimórficas y se disponen de forma subimbricada y/o yuxtapuesta.

4) Disposición de los órganos sensoriales (restringidos a las loreales en *L. josephorum* y extendidos hasta el subocular en *L. velosoi*, según Núñez *et al*. 2001): Los órganos sensoriales se presentan en el subocular en el 66,7% de los especímenes de *L. josephorum* (Fig1.c). En *L. velosoi* los órganos sensoriales se extienden al subocular en el 66,7% de los especímenes. No se encontraron diferencias significativas (*P* = 1,000).

5) Heteronotos en los flancos (presentes en *L. josephorum* y ausentes en *L. velosoi*, según Núñez *et al*. 2001): Todos los especímenes examinados presentaron heteronotos en los flancos. Más abundantes hacia la zona axilar.

6) Escamas dorsales del antebrazo: De acuerdo a Núñez *et al*. (2001), *L. josephorum* presenta escamas dorsales del antebrazo triangulares y quilladas (carácter que lo distinguiria de *L. velosoi* ya que esta especie presentaría escamas redondeadas quilladas y mucronadas, p. 104). Sin embargo en el mismo manuscrito, se menciona que las escamas dorsales del antebrazo en *L. josephorum* son redondeadas (carácter que lo distinguiría de *L. platei*, p. 103). Por lo tanto, estimamos que este carácter no puede ser tomado en cuenta como diagnosis. Nuestra observación muestra que las escamas dorsales del antebrazo pueden ser triangulares o redondeadas, siempre con quilla (algunas con mucrón) en ambas especies.

7) Escamas suprafemorales (lisas o ligeramente quilladas en *L. josephorum* y quilladas-mucronadas en *L. velosoi*, según Núñez *et al*. 2001): No se encontraron diferencias. Ambas especies poseen escamas dorsales femorales quilladas, algunas mucronadas.

8, 9 y 10) Banda occipital, banda parietal y línea supraocular (ausentes en *L. josephorum* y presentes en *L. velosoi*, según Núñez *et al*. 2001): Los especímenes adultos de ambas especies presentan estos caracteres, aunque el diseño de las hembras es notoriamente más difuso (Fig. 2, 3).

11) Garganta manchada (presente en *L. josephorum* y ausente en *L. velosoi*, según Núñez *et al*. 2001): Casi todos los especímenes de *L. josephorum* presentaron la garganta manchada (91,7%). Solamente un espécimen de *L. velosoi* presento la garganta manchada (11,1%). La diferencia es significativa (*P* = <0,001).

Discusión

Concordamos con Pincheira-Donoso & Núñez (2005) en que *L. josephorum* no muestra diferencias considerables respecto de *L. velosoi* para los caracteres diagnósticos propuestos por Núñez *et al*. (2001) y por lo tanto debe ser considerado un sinónimo junior de *L. velosoi*. La única diferencia significativa entre ambas poblaciones, que aún así muestra cierto solapamiento, es la presencia de garganta manchada en una mayor proporción de especímenes de *L. josephorum*, lo cual no justifica su clasificación como un taxón independiente y estimamos que más bien corresponde a una variación local en el diseño de coloración. De hecho, la misma variación fue encontrada en los especímenes de *L. platei*, que presentan una garganta sin manchas ni estrías en sus poblaciones más sureñas (Illapel y Coquimbo) y la garganta estriada en las poblaciones más norteñas (Llanos de Challe y Caldera).

L. josephorum fue descrito para Diego de Almagro, Finca de Chañaral y El Salvador, mientras que *L. velosoi* fue descrito para la cuenca del Río Copiapó, en las localidades de Monte Amargo, Piedra Colgada, Desvío Cerro Imán y Estación Paipote. Aunque ambas poblaciones se encuentran separadas por aproximadamente 90 Km (línea recta entre la Finca de Chañaral y Desvío Cerro Imán), no existe una barrera geográfica que impida el flujo génico entre ambas poblaciones y más bien parece que la falta de poblaciones intermedias obedece a una falta de muestreos (Fig. 4). En efecto, uno de nosotros (JTP), posee un registro fotográfico de un espécimen asignable a *L. velosoi* en la localidad intermedia de Inca de Oro, lo cual parece corroborar que este aparente "aislamiento" se debe a la falta de colectas (Fig. 3c).

L. velosoi puede ser distinguido de *L. platei* por la ausencia de mancha antehumeral (siempre presente en *L. platei*), escamas temporales lisas o débilmente quilladas (notoriamente más quilladas en *L. platei*) y dispuestas de forma subimbricadas-yuxtapuestas (nunca yuxtapuestas en *L. platei*), las escamas dorsales de *L. josephorum* son más grandes que las ventrales (similares en *L. platei*), el color de fondo de *L. josephorum* es gris-café (café-amarillento en *L. platei*), las manchas oscuras de la banda temporal son notoriamente más marcadas en *L. platei*, y de acuerdo a Pincheira-Donoso & Núñez (2005) la LS de *L. josephorum* varia entre 48,7 y 59,1 mm (entre 56,1 y 67,4 mm en *L. platei* de acuerdo a Pincheira-Donoso & Núñez, 2005).

Dentro del grupo "*nigromaculatus*" hay otras especies cuyo estatus taxonómico, o bien no está adecuadamente resuelto, o bien ha sido revisado recientemente. Pincheira-Donoso & Núñez (2005) proponen a *L. copiapoensis* (Müller & Hellmich, 1933) como sinónimo junior de *L. bisignatus* (Philippi, 1860) al considerar que las diferencias morfológicas y ecológicas entre ambas especies "*no son significativas como para establecer identidades evolutivas propias entre los dos taxa*"(p. 389). Estas especies habían sido encontradas como hermanas previamente por Lobo (2001) en un análisis filogenético. La sinonimia fue aceptada por Lobo *et al*. (2010) y nosotros también concordamos, ya que nuestro examen de topotipos de *L. copiapoensis* y *L. bisignatus* muestra que ambas poblaciones sobreponen sus caracteres diagnóstico. Por otra parte, Pincheira-Donoso &

Núñez (2005) propusieron que *Liolaemus kuhlmanni* (Müller & Hellmich, 1933) es un sinónimo de *L. zapallarensis* (Müller & Hellmich, 1933). Sin embargo, Lobo *et al.* (2010) rechazaron esta sinonimia debido a la falta de datos de respaldo ("*no supporting data presented*" p. 8). Creemos que es necesario llevar a cabo un estudio comparativo entre ambas especies para esclarecer la situación taxonómica de *Liolaemus kuhlmanni*.

Sin duda, el grupo *nigromaculatus* es uno de los clados con una de las historias taxonómicas más complejas de la herpetofauna nacional. Con este artículo, esperamos haber contribuido a esclarecer un poco su composición.

ANEXO

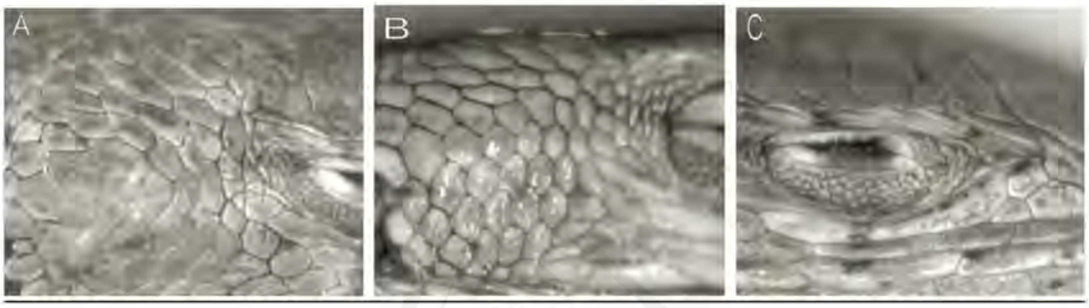

Fig. 01.
Detalle de algunos caracteres examinados. A) Escamas supratemporales en *L. josephorum* (SSUC Re 328). B) A) Escamas supratemporales en *L. velosoi* (MZUC 36624). C) Órganos sensoriales en el subocular de *L. josephorum* (SSUC Re 327).

Fig. 02.
Diseño dorsal de algunos especímenes examinados. A) Macho (izquierda) y hembra (derecha) de *L. josephorum.* B) Macho (izquierda) y hembra (derecha) de *L. velosoi*.

Fig. 03.
Fotografías de especímenes en vida. A) *L. josephorum*, Diego de Almagro. B) *L. velosoi*, Tierra Amarilla (10 Km al sur de la localidad tipo). C) Espécimen de *Liolaemus* con el diseño típico de *L. josephorum* y *L. velosoi*, fotografiado en Inca de Oro (localidad intermedia entre las distribuciones conocidas de ambas especies).

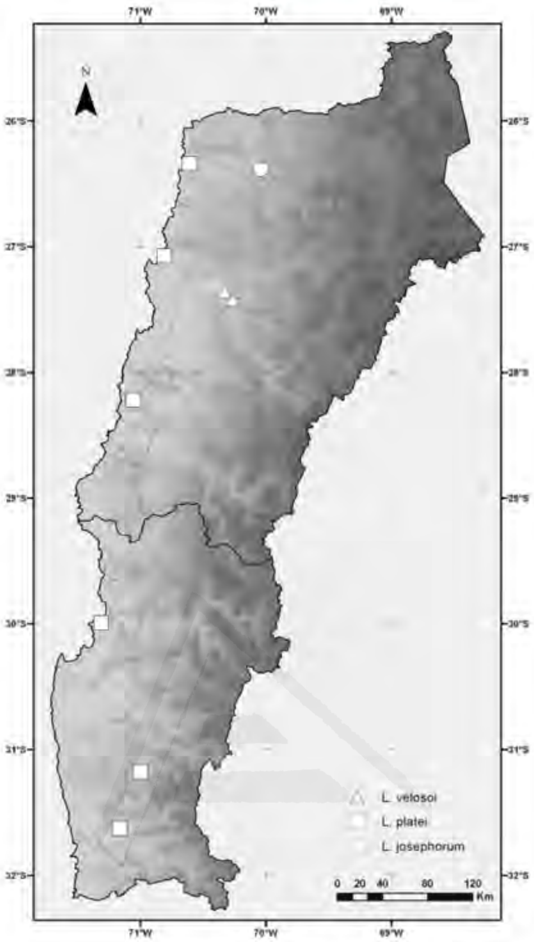

Fig. 04.
Mapa de las localidades de procedencia de los especímenes usados en este estudio.

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Apendice I: Especímenes examinados

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A Regional Climate Study of Heat Waves over the Iberian Peninsula

Hari Prasad Dasari[1]*, Isaac Pozo[2], Francisco Ferri-Yáñez[2,3,4], Miguel B. Araújo[2,3,4]

[1]Centro de Geofisica de Évora, University of Évora, Évora, Portugal
[2]Museo Nacional de Ciencias Naturales, CSIC, Madrid, Spain
[3]Centro de Biodiversidade e Recursos Genéticos (InBIO-CIBIO), University of Évora, Évora, Portugal
[4]Imperial College London, Silwood Park Campus, Berkshire, UK
Email: *hari@uevora.pt, ipozo@mncn.csic.es, francisco_ferri@mncn.csic.es, maraujo@mncn.csic.es

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Abstract

We present a regional climate simulation for the Iberian Peninsula for a 60-year period (1950-2009) using the WRF-ARW model with a focus on the simulation of summer maximum temperatures and associated extreme heat waves. The WRF model was designed at a 5 km horizontal resolution on a 5-month (May-September) seasonal scale, for every year, during the study period with initial/boundary conditions derived from NCEP 2.5 degree reanalysis. The comparison of simulated mean summer seasonal maximums and mean maximums of June, July, and August months with the corresponding E-OBS data sets indicates that the model is able to characterize the spatial variation of magnitudes of temperature change over the Iberian Peninsula. The mean extreme heat wave conditions during the climate period 1950-2009 are well simulated and match the observations well. The regional scale simulations clearly show the propagation of intense heat waves from the south west to north east of Iberia. The WRF-ARW model also simulated well the general trend of increase in heat waves over most parts of the Iberian Peninsula during the study period 1950-2009. The characteristics of the most severe heat waves years 2003 and 2006 are also well simulated by the model.

Keywords

Downscaling, Heat Waves, Iberian Peninsula, Regional Climate Modelling

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*Corresponding author.

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1. Introduction

The Iberian Peninsula falls in the transition zone of tropical and extra tropical climates with more than 80% of days of clear sky and sunshine. The region is usually influenced by the cold temperatures of the Atlantic Ocean and the warm temperatures over the Mediterranean Sea and the Sahara desert. Because of the peculiar geography of this region, there is a marked north-south climate gradient as well as a gradient of increased diurnal and seasonal thermal variation from the coastal areas to the centre of the Peninsula. High mountain ridges in the northern limits of the Peninsula also influence the regional weather and climate, while acting as barrier between northern and southern Europe.

Several studies have reported an increase in the frequency of heat waves in Europe and models forecast even higher frequency by the end of the 21st century [1] [2]. Many reasons have been proposed for such increase in the frequency of heat waves in Europe. One reason is related to the general warming due to increased green house gases from anthropogenic activities [3]. Climate model projections indicate that increases in annual mean temperatures with higher warming in the winter over northern Europe and in the summer over the Mediterranean area [4]. Tebaldi *et al.*, [5] reported that maximum summer temperatures in southern and central Europe are likely to increase more than mean temperatures. Another reason is the movement of anti cyclonic weather regimes to form heat waves in Europe. Cassou *et al.* [6] reported that the synoptic Rossby wave trains from tropical Atlantic sea surface temperatures are favourable conditions to form heat and drought conditions over Europe. Della Marta *et al.* [7] reported that apart from the synoptic conditions the feedbacks from regional land surfaces act positively to amplify the summer maximum temperatures over Europe. Other factors like heat advection, cloud cover, radiation and moist convection also contribute to increasing summer temperatures [8]. The soil-atmosphere feedbacks were studied during four severe summer seasons by Ficher *et al.* [9] [10]. It has been reported that dry soil promotes a positive feed-back mechanism of anticyclone conditions by reducing the moist convection, reducing clouds and increasing the solar energy at the surface thereby further increasing the heat fluxes and the Bowen ratio [11]. D'Andrea *et al.* [12] suggests that even though the soil moisture is a key factor in controlling summer mean temperatures there is little work done on the physical process involved in it. Vautard and Coauthorset [13] analysed the 10 hottest summers since 1948 revealing that hot summers can occur after normal or wet winter and spring conditions in the north and drier soils in Southern Europe.

High resolution Regional Climate Models (RCMs) with improved physics in respect of clouds, land surface, boundary layer diffusion and convection process have shown to be useful to simulate regional climate. The major advantage in using RCMs is the inclusion of regional effects of topography, coastlines, mountains, water bodies, and vegetation on the local climate [14]-[28]. The focus of this study is to simulate the extreme temperatures and heat wave conditions over the Iberian Peninsula using the WRF regional model [29] and evaluate it through hindcasting using available 20th century climate data.

We chose this model because of its sophisticated physics for land-surface, planetary boundary layer, radiation and other atmospheric processes that are important to simulate regional and small-scale atmospheric processes affecting climate. The temperature patterns over the Iberian Peninsula, their long-term variability and the sub-regional variations, are simulated with a nested regional model at 5 km resolution along a 60-year period (1950-2009) for the summer seasons.

2. Model and Data

In this study we used the Advanced Research Weather Research and Forecasting (ARW) regional model [29] to simulate long-term temperatures over the Iberian Peninsula. The model uses non-hydrostatic compressible Navier-Stokes equations for the atmosphere in a terrain following sigma coordinate system. The model is highly flexible for choosing the domain region with multiple nested domains, physics and diffusion options. The model is configured with two-way interactive two-nested domains with horizontal grid resolutions of 75 km and 25 km. One-way nesting is used in generating a 5 km resolution from the 25 km resolution result. The domain area and design of the three domains is presented in **Figure 1**. The model physics and other details are presented in **Table 1**. The outer domain covers the entire Europe and parts of the Atlantic Ocean, and Southern arctic. The inner domain with 5 km horizontal resolution covers the Iberian Peninsula alone. We used the National Centers for Environmental Prediction (NCEP) global analysis fields [30], available at 2.5 degree latitude/longitude resolution and at 6-hour interval, for initial atmospheric fields and the time varying boundary conditions. The model was integrated continuously for 5 months, starting at 00UTC of the 1st of May for each year starting in 1950 and

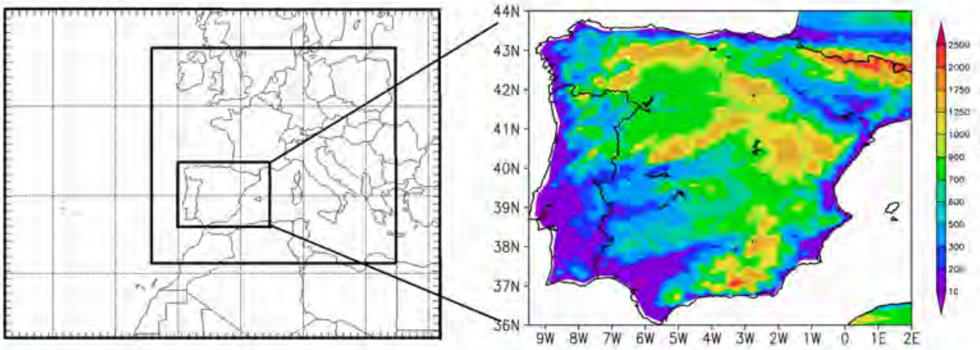


Figure 1. Model chosen domains with topography.

Table 1. Model details and configuration.

Model Name	NCEP/NCAR ARW		
Model type	Primitive equation, non-hydrostatic		
Vertical resolution	30 sigma levels		
Horizontal resolution	75 km	25 km	5 km
Domain of integration	38.5W - 30.83E 21.82N - 59.75N	13.585W - 24.8351E 31.7935N - 55.7455N	9.429W - 3.037E 35.947N - 43.98N
Radiation scheme	CAM scheme for short wave radiation CAM scheme for long wave radiation		
Land-surface scheme	Thermal diffusion scheme		
Sea surface temperature	Real sea surface temperatures		
Convection scheme	Grell-devenyi ensemble scheme		
PBL scheme	YSU scheme		
Explicit moisture scheme	WSM 3-class simple ice scheme		

continuing for the entire 6 decades (1950-2009). This procedure aimed at improving the knowledge of the temperature variations in the summer seasons (June, July and August) linked to extreme heat events over the Iberian Peninsula. The model outputs were generated at 1-hour intervals keeping in mind the need of high-resolution temporal data in several climate change impact studies, such as the case of biodiversity [31]. The first month results in all simulations were considered as a spin-up time and were not used for analysis. The daily maximum temperatures were computed from the 1-hour interval outputs. The model results for the whole 60-year period (1950 to 2009) were compared with E-OBS V7.0 [32] observations available at 0.25 degrees. It is important to note that no corrections for E-OBS datasets have been made and Soares *et al.*, [33], reported deficiencies with this data source.

3. Results and Discussion

The results are presented in three sections. The first section focuses on 60-year mean values of maximum temperatures for summer season (JJA) and individual months of June, July and August, all of which are computed and analysed for both model and E-OBS. In this section we also focused on the variability of maximum temperatures for pre-industrial and post-industrial era based on the reference period (1961-1990). In the second section the mean extreme summer heat wave conditions for the years 1950, 1952, 1959, 1964, 1976, 1983, 1992, 1994, 1995, 2003 and 2006 are discussed for the Iberian Peninsula. The extreme summer heat wave years are taken from Vautard *et al.* [13]. Finally, in Section 3, a critical analysis is made for the two most recent extreme heat waves of 2003 and 2006. Heat wave conditions are computed using daily maximum temperatures from summer months as per the definition for heat waves prescribed by World Meteorological Organization.

3.1. Mean Maximum Temperature Analysis

Observations indicate a concentric distribution of maximum temperatures with higher temperatures in the south. Temperature comparisons with observations indicate that the spatial distribution of seasonal mean maximum temperature is well represented by the model (Figure 2). The warmer temperatures over southern Iberian Peninsula and the colder regions along northern and north-eastern mountain ranges are well reproduced. Unlike in interpolated observations, the model shows the fine scale variations in temperatures related to location specific variations of surface/terrain variables. The regional variations in the mean maximum temperatures are well depicted by the model, which shows the advantages of using the high-resolution regional climate model. The smaller number of contours in observations could be because of less number of observations used in preparing E-OBS data. The differences in the seasonal mean maximum temperature between pre-industrial period (*i.e.* the period of 1950-1975), and the reference period (*i.e.* 1961-1990), as well as between post-industrial period (*i.e.* the period of 1976-2009) and reference period are computed for both model and observations. The changes in summer mean maximum temperatures before and during industrial period shows that at pre-industrial times, the change in summer seasonal maximum temperatures with respect to reference period in the model is almost negligible (**Figure 2(c)**), while some few regions over Iberian Peninsula seem (Figure 2(d)) to have increased its temperature up to 0.25˚C. This may be due to rapid urbanization process during this period that affected several regions of the globe along with Iberian Peninsula, a process that may not be well represented in the model due to the use of static land use datasets in the model domain. With the exception of these relatively small numbers of areas the model shows no change in temperature. We find that during post-industrial period the changes in temperatures are very significant in both model and observations (Figure 2(e) and Figure 2(f)). Simulation shows an increase of 0.25˚C - 0.50˚C rise in temperature over the entire Iberian Peninsula with larger changes over the south and southeast part of Iberian Peninsula (>0.5˚C). In southern parts of the Iberian Peninsula and over Portugal region a temperature increase of 0.5˚C is simulated. While model simulation is good over the southern parts, it underestimated the changes in maximum temperatures by ~0.5 ˚C in the central and north-eastern regions.

An analysis of temperature changes in each month during pre- and post-industrial periods with respect to reference period are presented enabled us to explore departures from climate average conditions and study the heat waves in summer months. The analysis shows that while observations indicate a slight increase of 0.25˚C in pre-industrial era in the month of June (Figure 3), those changes are negligible (Figure 3(a)). A large increase of temperature is noticed in the post-industrial period both in observations and simulations. Model temperature changes are about 0.25˚C lower than the corresponding changes estimated from observations over entire Iberian region. A few exceptions are found over Lisbon and adjacent southern coastal regions. There is an increase of over 1˚C over northern Spain and few selected regions in the south. The mountain regions and entire Mediterranean coast and northern coastal regions show an increase of 0.5˚C. Observations indicate that the entire Iberian region is showing an increase of 1˚C, except for some coastal regions and over some mountain regions that show an increase of 0.5˚C. In this analysis also it is very clear that the observations are more uniform way of increase in temperature and it is not showing changes on local to regional scale. This is because of the E-OBS data is of with 25 km grid resolution, where as the model is able to generate most of the regional features very well. Alternative high-resolution observations were unavailable at the time of this study for more comparisons.

Similar results to the June observation-simulation comparison are obtained when the month of July is examined. In July the mean maximum temperatures during pre-industrial period did not change in the model (**Figure 4(a)**) but some of the southern parts have increased about 0.5˚C in observations (Figure 4(c)). The rest of Iberia shows no change. In the post-industrial period, on the other hand, the mean maximum temperatures from the model (**Figure 4(b)**) and observations (Figure 4(d)) show a significant increase of 0.25˚C to 1˚C. In the southern parts of the Iberian region the model results show an increase of 0.5˚C, which are well matches with observations. In northeast region, on the other hand, the observations show an increase of 0.75˚C and, in some isolated pockets, an increase of 1˚C that is not captured by model. Northern Portugal and adjoin regions with lower temperature and southern Iberian with higher temperature patterns are well represented by the model and with good agreement with observations. A difference of ~ 0.25˚C maximum temperature changes is noted between model and observations for July.

In August, the models show some coastal regions of Mediterranean and northern Iberian regions have a slight increase in temperature during the pre-industrial period (Figure 5(a)). A similar trend is noticed in the observations (Figure 5(c)), with a slight increase over Mediterranean coastal region and with no significant changes iden-

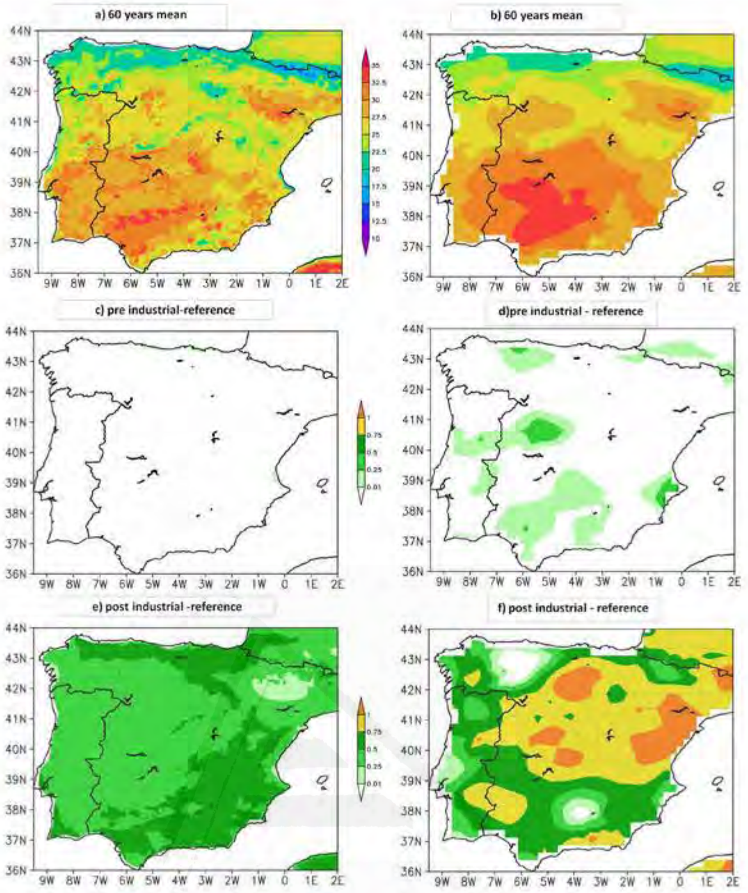


Figure 2. Mean seasonal maximum temperatures for 60-year period. Differences between mean seasonal maximum temperature for pre-industrial and post-industrial periods from the reference period (1961-1990). Left panel is for model and right panel is for observations.

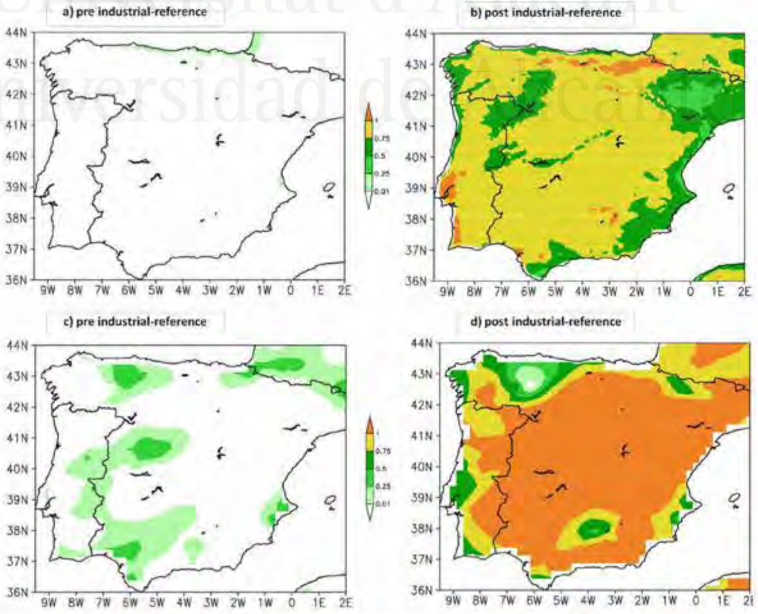


Figure 3. Differences between mean June month maximum temperature for pre-industrial and post-industrial periods from the reference period of 1961-1990. Top panel is for model and bottom panel is for observations.

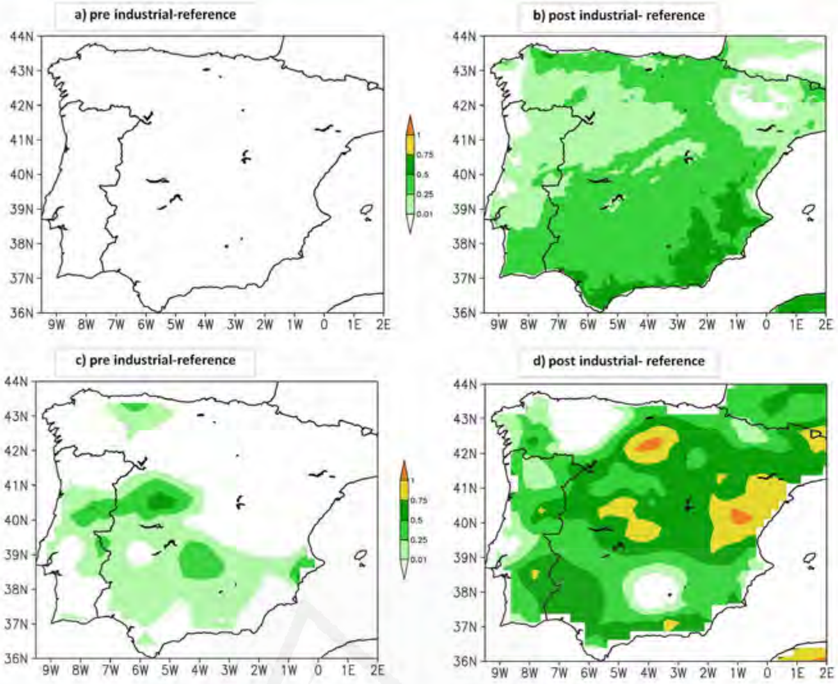


Figure 4. Differences between mean July month maximum temperature for pre-industrial and post-industrial periods from the reference period of 1961-1990. Top panel is for model and bottom panel is for observations.

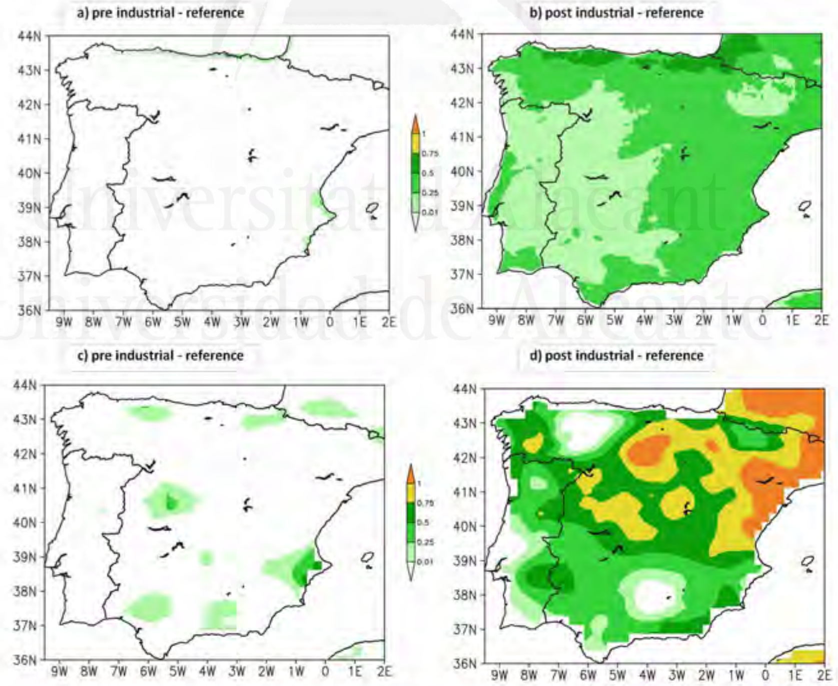


Figure 5. Differences between mean August month maximum temperature for pre-industrial and post-industrial periods from the reference period of 1961-1990. Top panel is for model and bottom panel is for observations.

tified in the rest of the whole Iberian. In contrast to the pre-industrial era, the post-industrial period shows a temperature increase in (**Figure 5(b)** and **Figure 5(d)**) south and south-eastern parts of Iberia in both simulations and observations. The increase is noticed in both model and observations from southern Portugal and south-western Iberia, towards north and north eastern Iberia. The increase is in the range of 0.25˚C to 0.5˚C in the model where and of 0.25˚C to 1˚C in observations. The model underestimates for an amount of 0.25˚C to 0.5˚C from south to north and north-eastern region.

3.2. Mean Maximum Temperature Analysis for Extremely Heat Wave Years

Next we examine 11 years of severe heat waves between 1950-2009. This 60 years period was chosen based on a previous study by Vautard *et al.* [13] that identified 10 extreme summer heat wave conditions during the same period. The heat waves occurred in 1950, 1952, 1959, 1964, 1976, 1983, 1992, 1994, 1995 and 2003. We also added the recent heat wave of 2006. These 11 years are used to identify the abnormal changes in temperatures that occurred in comparison with reference period. For this analysis we used the monthly mean maximum temperatures for both model and observations.

The model shows a very clear increase in temperature, with significant regional changes, for June monthly mean temperatures in the 11-year period with severe heat waves (Figure 6(a)). The model shows more than 32.5˚C over many parts of the southern and some north-eastern parts of Iberian Peninsula. A good pattern comparison is found in ARW simulation for the extreme year summer temperatures as in observations. The observations show (Figure 6(b)) that the temperatures are around 30˚C in southern parts and are still low in north-eastern part of Iberian Peninsula. Interestingly, the model shows very fine scale regional temperature patterns that are not identifiable from interpolated observations. The change in mean heat wave June maximum temperatures is quite significant in both model and observations (Figure 6(c) and Figure 6(d)) with regard to reference period. The change of 0.5˚C to 2˚C is noticed in both model and observations although with spatial variability. In the model, there is an increase of 2˚C over Lisbon region, about 1˚C over south of Portugal, 1.5˚C over and north of Portugal and about 1˚C to 1.5˚C towards north and northeastern Iberia. In the south of the Iberian Peninsula the model temperature changes are about 0.01˚C to 0.5˚C. In observations, the increasing trend from southern Portugal to north and north-eastern Iberian Peninsula matches well the model but with an intensity of about 0.5˚C higher. Observations show that almost all of the Southern and north-eastern Iberian Peninsula has increased by 1˚C to 1.5˚C and north eastern parts by 1.5˚C to 2˚C. Mean temperatures in July have increased more than those of the previous month, as it is expected, in both model and observations (Figure 7(a) and Figure 7(b)). Mean temperatures of more than 35˚C are noticed in both model and observations but in the model, clear regional changes at local scales are apparent. The change in temperatures from the reference period shows a clear increasing trend from the south-west to the north-east of the Iberian Peninsula in both model and observations. The range of increase is of about 0.01˚C to 1˚C in the model while it is 0.01˚C to 1.5˚C in the observations. A similar pattern as in July is noticed in August in both model and observations, with slightly lower intensity in mean severe summer temperatures (Figure 8(a) and Figure 8(b)) and with lesser changes in temperatures (Figure 8(c) and Figure 8(d)) with respect to the reference period. These results show that while the extreme high temperatures in Iberian Peninsula are found in July, June temperatures are the ones that increased the most in the season of JJA. That is very clear from the changes in both 60-year mean maximum temperatures and extreme heat wave mean June temperatures with respect to the reference period. In July and August, the magnitude of changes is than in June. June changes are higher in the south of Portugal and north-western Iberia and in the other two months the shift moves towards north and north eastern parts of Iberian Peninsula. This phenomenon matches well the observations. It is very clear in model results that there are large changes in extreme temperatures in Iberian Peninsula, particularly in the southern parts and in June and moving towards north-eastern parts of Iberia in July and August. These fine features are not noticeable with the observations probably because of the number of observations considered in preparing the E-OBS data. The fine scale features are well noticed in the model because of the advantage of using a high resolution RCM. The increase of temperature changes over north-eastern parts of Iberian Peninsula may be because of heat advection due to anticyclonic circulations, significant changes of landuse/vegetation which may influence by changing albedo, emissivity factors and rapid urbanization.

3.3 Mean Maximum Temperature Analysis of the Latest Heat Wave Years (2003 and 2006)

We used 10-day daily maximum mean temperatures for both 2003 and 2006 to understand the duration of heat waves. In 2003 (Figure 9), the heat wave conditions were detected from 10th of June onwards extending to the last week of the month. The total duration was of about 15 to 20 days and it was noticed in almost all areas of Iberian Peninsula except the northern parts. After a 10-day gap a second spell became apparent from 10-20 July in most of

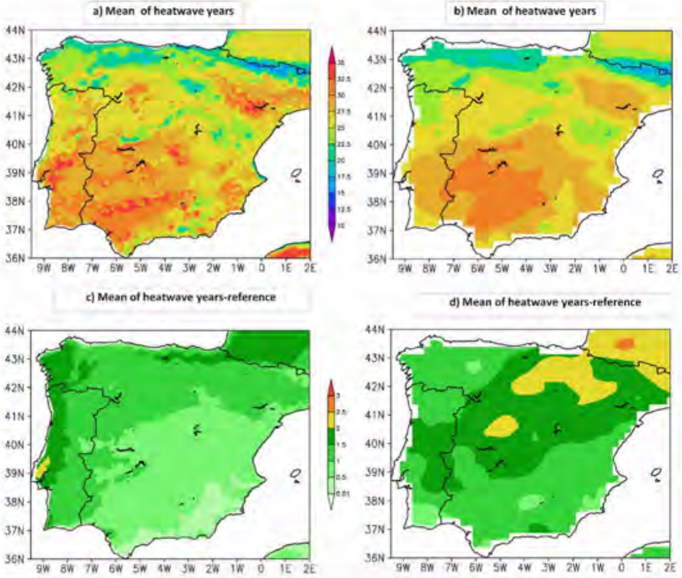


Figure 6. Mean June month maximum temperatures for extreme heat wave years (top panel). Differences between mean June month maximum temperatures for extreme heat wave years from the reference period of 1961-1990 (bottom panel). Left panel is for model and right panel is for observations.

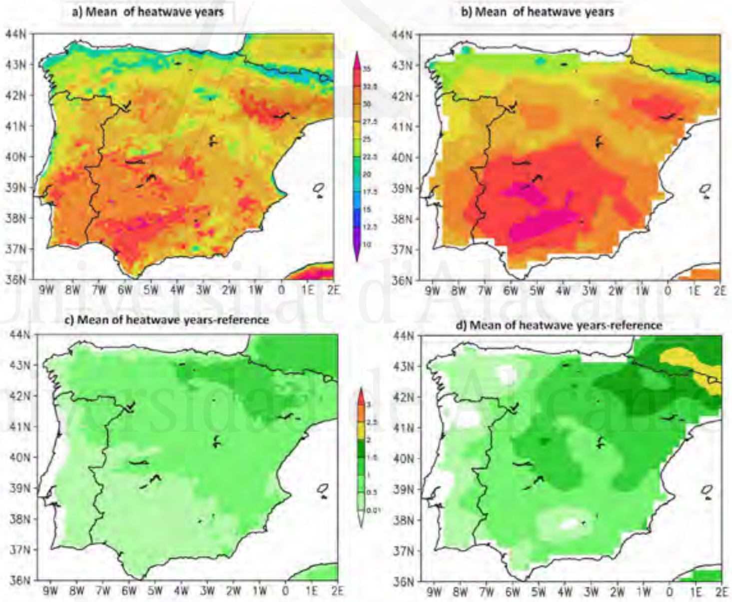


Figure 7. Mean July month maximum temperatures for extreme heat wave years (top panel). Differences between mean July month maximum temperatures for extreme heat wave years from the reference period of 1961-1990 (bottom panel). Left panel is for model and right panel is for observations.

the southern parts of the Iberian region and it moved still further south for another 10 days; after that it spread over the entire Iberian Peninsula. The heat wave conditions persisted over nearly 50 days with small gaps starting from second week of July to the last week of August. Because of the length of this severe heat wave conditions over Iberian region, several heat-wave related deaths and forest fires were reported over the region. In 2006 heat wave conditions were not very apparent in June. Mostly, heat wave conditions prevailed from 10 July over the south-west of the Iberian Peninsula and they slowly extended to the north-eastern parts of Iberian Peninsula by end of July with increased intensity. The mean temperatures reached almost 40˚C and the severity of the heat wave (**Figure 10**) was much higher (by ~5˚C) than that of 2003. But the duration of heat wave conditions in 2006 were

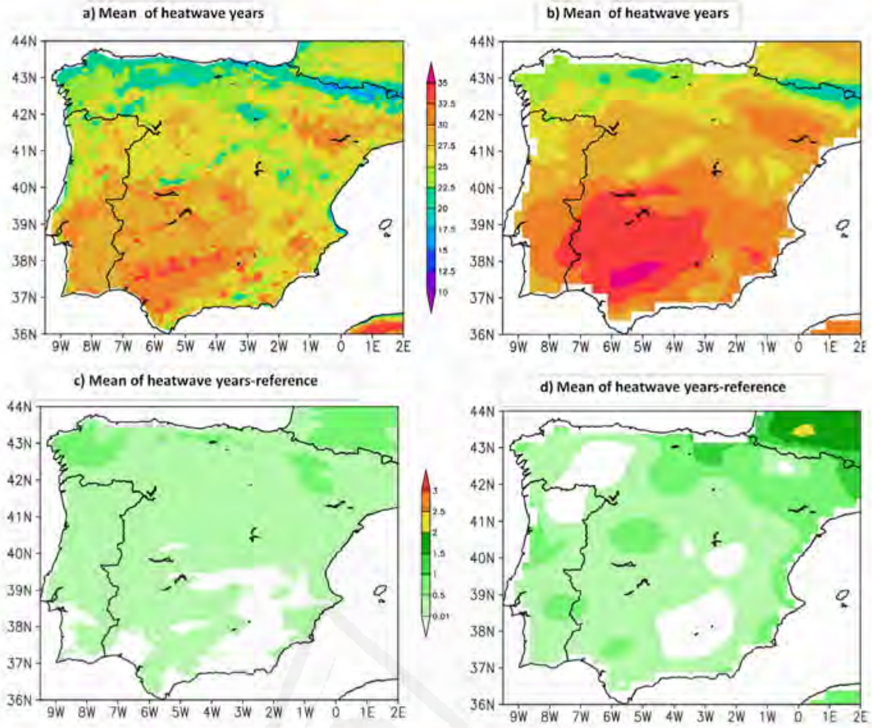


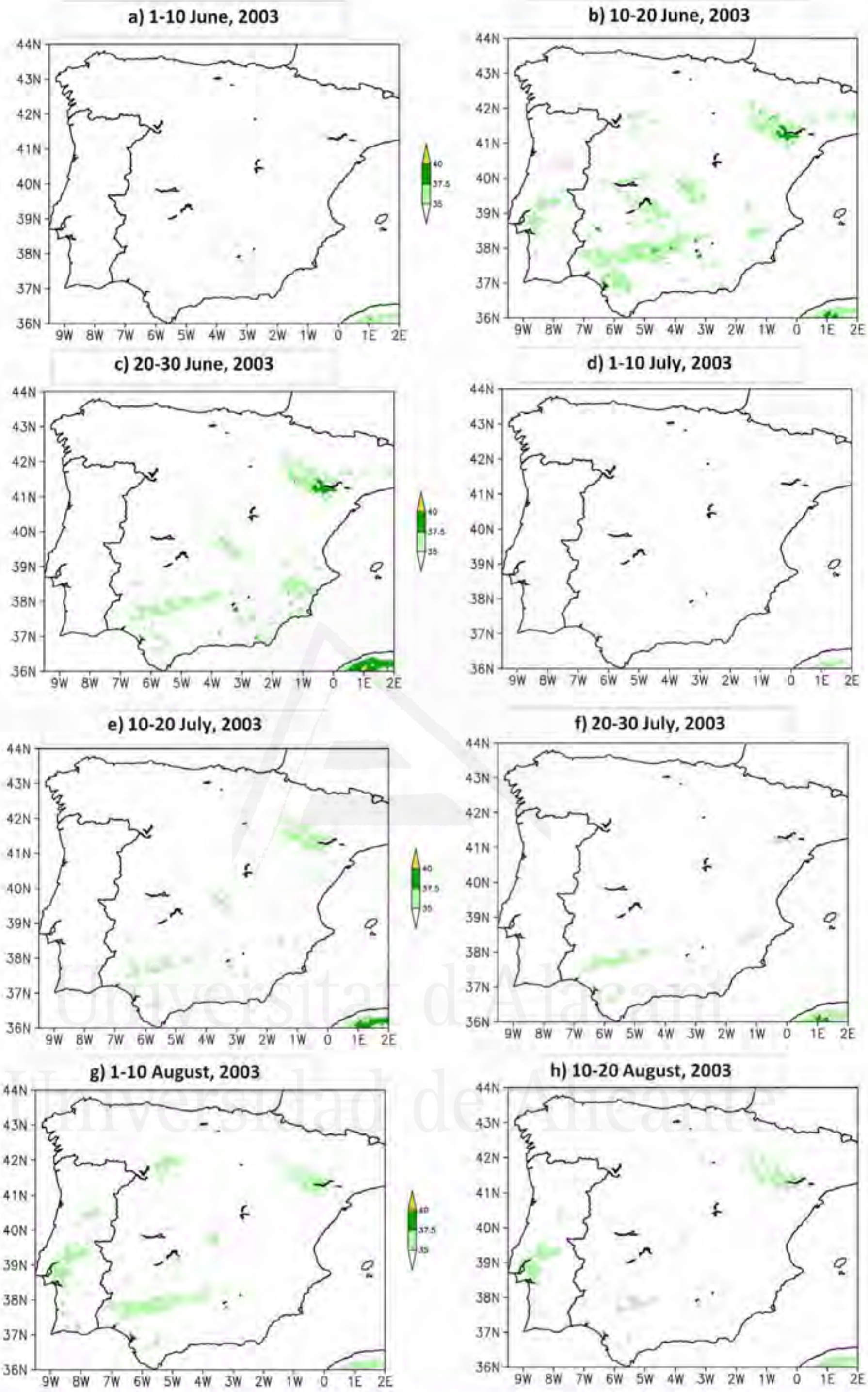
Figure 8. Mean August month maximum temperatures for extremely heat wave years (top panel). Differences between mean August month maximum temperatures for extremely heat wave years from the reference period of 1961-1990 (bottom panel). Left panel is for model and right panel is for observations.

of about 25 days starting from the second week of July to the first week of August, while that of 2003 lasted for nearly 50 days. The heat wave temperatures were much higher in 2006 than in 2003 over the southern parts of Iberian Peninsula. There were two continuous spells of heat wave conditions in 2003, one in June and the other one in July while in 2006 one continuous spell of heat wave from second week of July prevailed.

4. Summary

The ARW model is used to simulate the regional heat wave conditions over the Iberian Peninsula related to extreme maximum temperatures over a 60-year climate period. A RCM is used at a high spatial and temporal resolution (5 km, 1 hour) and model temperature climate is compared with the E-OBS data set. The analysis of the maximum temperatures is made over summer season (June-August) considering the reference period 1961-1990 with breakups of pre and post industrial eras to identify the corresponding temperature changes. The results indicate that the temperatures have significantly increased in the post industrial era, which agrees with results reported in many other studies. The summer mean maximum temperatures increased about 0.5˚C after industrialization over most parts of Europe which agrees with the observations. Temperature changes are larger in June than in July and August. The June month temperatures increased by 1˚C - 1.5˚C over most parts of the Iberian Peninsula whereas July and August temperatures increased by 0.25˚C - 0.75˚C. These model results reasonably agree with observations, which are spatially smooth due to interpolation of sparse point data sets. The model realistically simulated the fine scale summer temperature changes over the entire Iberian Peninsula.

Extreme heat waves of 11 years are chosen during this 60-year period to understand the model capability to simulate extreme hot conditions. The 11-year mean seasonal heat wave conditions are well simulated by the model and with good agreement. The propagation of severe hot condition towards the north western region of Iberian Peninsula as in observations is well simulated by model. An increase is of 0.5˚C to 2˚C in both model and in observations is found over the study domain. Especially the increase of temperatures in June indicating extreme heat wave conditions over north eastern parts of Iberian region relative to July and August is well produced by model. Analysis of various parameters shows that the model captured the mean heat wave conditions found in



a) 1-10 June, 2003

b) 10-20 June, 2003

c) 20-30 June, 2003

d) 1-10 July, 2003

e) 10-20 July, 2003

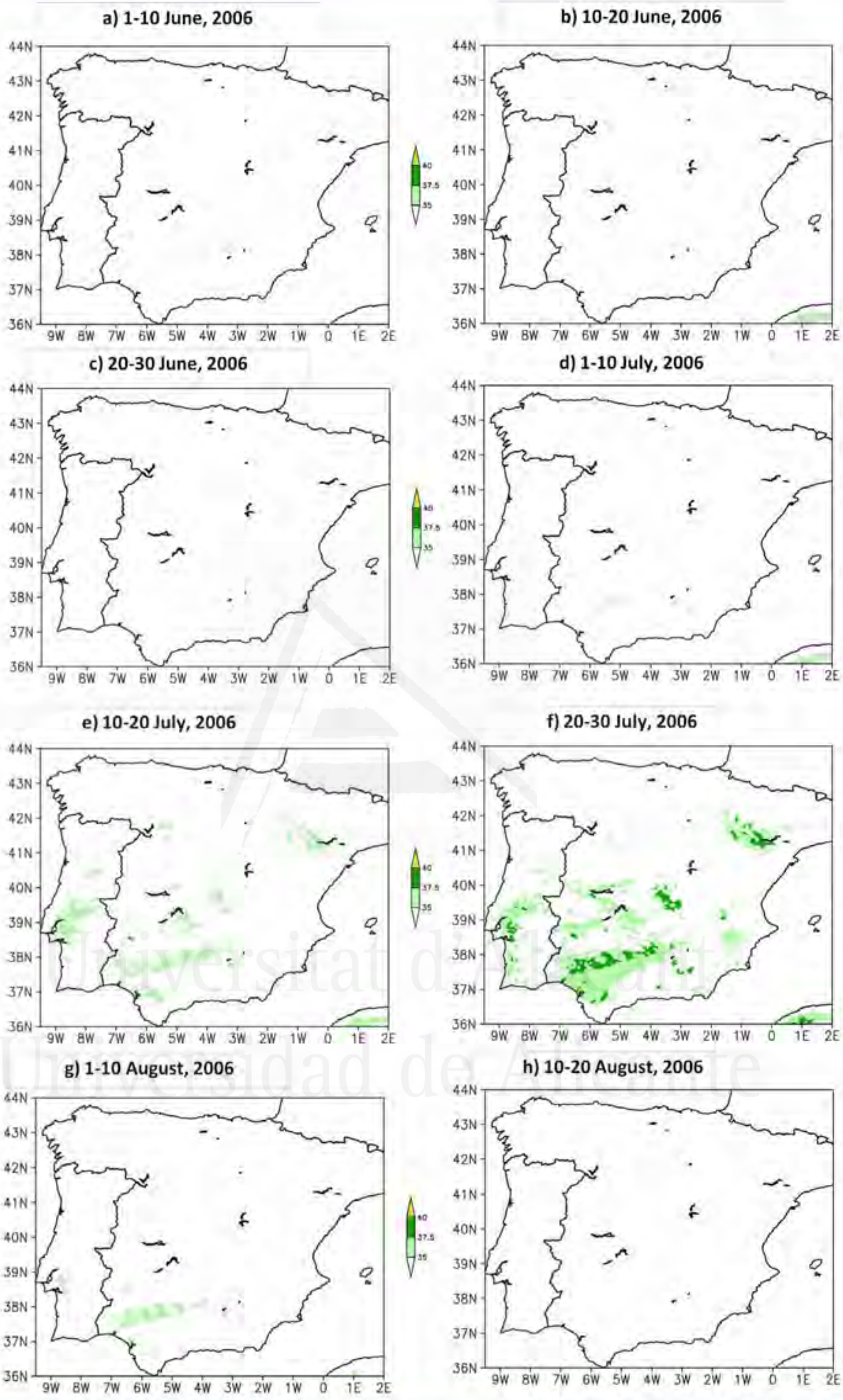
f) 20-30 July, 2003

g) 1-10 August, 2003

h) 10-20 August, 2003

Figure 9. Model produced 10-day mean maximum temperatures for 2003 summer (more than 35˚C only plotted).

E-OBS observations. Analysis of two extreme years indicated that the heat wave of 2003 has two spells one in June and other one in July. The total length of these heat conditions sustained for about 50 days with mean maximum temperatures of more than 40˚C. In 2006, the heat wave conditions persisted for about 25 days starting in the beginning of the second week of July. The model simulated the higher intensive heat wave conditions in 2006 relative to 2003 in agreement with observations. The progress of heat wave conditions from south western



a) 1-10 June, 2006

b) 10-20 June, 2006

c) 20-30 June, 2006

d) 1-10 July, 2006

e) 10-20 July, 2006

f) 20-30 July, 2006

g) 1-10 August, 2006

h) 10-20 August, 2006

Figure 10. Model produced 10 day mean maximum temperatures for 2006 summer (more than 35˚C only plotted).

parts to north eastern parts of Iberian region is well produced by the model.

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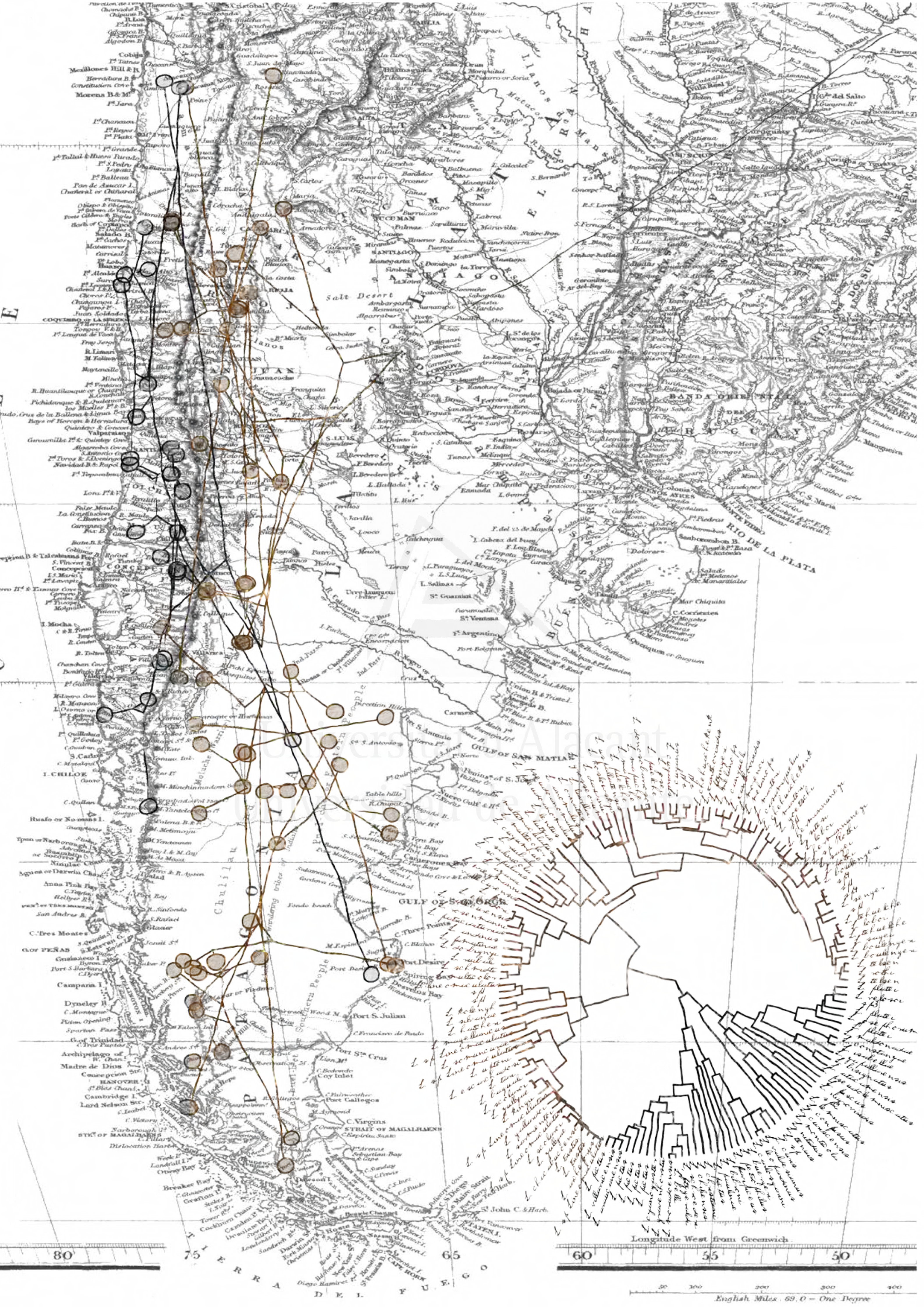
Salt Desert
GULF OF SAN MATIAS
GULF OF S. GEORGE
RIO DE LA PLATA
BANDA ORIENTAL
STRAIT OF MAGALHAENS
I. CHILOE
Port Desire
Port S. Julian
Port Gallegos
C. Virgins
STATEN I.
CAPE HORN
TIERRA DEL FUEGO
Longitude West from Greenwich
80
75
65
60
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English Miles 69,0 = One Degree