TESIS DOCTORAL

Reglas ecológicas de ensamblaje en comunidades de plantas de alta montaña

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CERTIFICAN:

Que los trabajos de investigación desarrollados en la memoria de tesis doctoral: "**Reglas ecológicas de ensamblaje en comunidades de plantas de alta montaña**", han sido realizados bajo su supervisión y son aptos para ser presentados por el licenciado Jesús López Angulo ante el tribunal que en su día se consigne, para aspirar al Grado de Doctor en el Programa de Doctorado de Ciencias por la Universidad Rey Juan Carlos.

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Resumen

Antecedentes

Uno de los mayores desafíos que se vienen planteando los científicos desde el inicio de la Ecología es identificar los mecanismos responsables del ensamble de comunidades de plantas y esclarecer los determinantes que conducen la coexistencia local de las especies. Pese al esfuerzo realizado en construir un marco unificador que establezca cómo se ensambla la diversidad de plantas en las comunidades, el éxito ha sido relativamente escaso, y gran parte de culpa lo tienen ciertas limitaciones tanto descriptivas como analíticas.

El hecho de que los patrones de diversidad y sus determinantes varíen a diferentes escalas espaciales dificulta en muchas ocasiones el alcance de respuestas generales y hace que se obtengan resultados discrepantes cuando se intentan responder las mismas preguntas. Por tanto, para atajar eficazmente las preguntas relacionadas con el ensamble de comunidades de plantas es necesario aplicar un enfoque metodológico que permita el estudio simultáneo de un conjunto de escalas espaciales. A la problemática de las escalas, se suma la limitación de la que adolece una de las aproximaciones más usadas en ecología, la perspectiva taxonómica, que tiene que ver con la asunción subyacente de que todas las especies son funcionalmente equivalentes y evolutivamente independientes. De este modo, resulta ineludible la evaluación de las diferencias ecológicas y evolutivas que hay entre las especies de la comunidad para facilitar la manifestación de procesos ecológicos y evolutivos que determinan la composición de especies de la comunidad.

Algunas limitaciones analíticas están asociadas con el uso de modelos nulos que tienen capacidad reducida para detectar procesos ecológicos específicos. Así surge la necesidad de avanzar hacia el desarrollo de algoritmos que tengan en cuenta las probabilidades de incidencia de las especies bajo una determinada fuerza ecológica para detectar la prevalencia de otros mecanismos no considerados por el algoritmo. Otra restricción en el avance en este campo tiene que ver con el hecho de que las respuestas   de

las comunidades de plantas a factores locales y los procesos subyacentes son muy idiosincráticos y varían a lo largo de los distintos sistemas montañosos debido a características regionales como el clima o la historia evolutiva de las especies de la comunidad. Por tanto, para comprobar si las respuestas de la comunidad al ambiente son generales o inherentes a las condiciones climáticas y la historia evolutiva, y así avanzar hacia un marco global, se deberían de plantear las mismas preguntas en contextos regionales, pero con climas contrastados, y por otro lado en regiones con historias biogeográficas distintas pero con climas similares

Objetivos

Nuestro objetivo es intentar arrojar luz en búsqueda de las reglas ecológicas de ensamblaje en comunidades de plantas de alta montaña y la identificación de los principales mecanismos responsables que estructuran la diversidad, prestando especial atención a algunas de las limitaciones que restringen el progreso hacia un margo global para la teoría de coexistencia como son el problema de la escala espacial, la elección de modelos nulos adecuados y eficaces, y la replicación del estudio en regiones con distintas condiciones climáticas e historias biogeográficas.

Metodología

El estudio se centró en las comunidades plantas de alta montaña de cuatro cadenas montañosas, las cuales presentan diferente clima y/o historia evolutiva y biogeográfica. En España se muestrearon (1) 39 sitios en el Parque Nacional de la Sierra de Guadarrama influenciado por el clima Mediterráneo y (2) 27 sitios en el Parque Nacional de Ordesa-Monte Perdido con clima templado. Otras dos regiones fueron muestreadas en la cordillera andina en las que se muestrearon (3) 20 sitios en los alrededores del Valle Nevado y la Laguna del Maule en los Andes centrales de Chile e influenciado también por un clima Mediterráneo y (4) 17 sitios en el Parque Nacional Torres del Paine en el sur de la Patagonia caracterizado tipo por un clima Sub-antártico. En cada cadena montañosa se muestreamos a 3 escalas distintas las comunidades de plantas que se encuentran por encima del límite arbóreo cubriendo el gradiente altitudinal completo donde se produce este de ecosistema.

En cada unidad muestral se estimó la cobertura de cada especie. Cada sitio fue caracterizado por su altitud, la insolación incidente, la fertilidad del suelo y la

prevalencia de las interacciones entre especies. Con todas las especies presentes en todas las cordilleras construimos un árbol filogenético utilizando dos loci (rbcL y matK) para caracterizar la estructura filogenética de las comunidades. Por otro lado, se midieron 7 rasgos funcionales que esperamos que respondan a las condiciones ambientales, para las especies más abundantes en cada cordillera: (i) la altura vegetativa máxima (Hmax), (ii) el tamaño de la planta (IS), (iii) el área foliar específica (SLA), (iv) el contenido de materia seca foliar (LDMC), (v) el grosor de la hoja (LT), (vi) el área de la hoja (LA) y el peso de la semilla (SM). Con la información de abundancias, el árbol filogenético y los rasgos, se calcularon índices de diversidad taxonómica, funcional y filogenética. La respuesta de estas métricas a los factores ambientales fue estudiada principalmente usando modelos lineales y modelos de ecuaciones estructurales.

Resultados

La riqueza de especies respondió de manera unimodal a la altitud a lo largo de distintas latitudes de los Andes Chilenos cuando fue evaluada a escalas grandes. Otros factores como las interacciones bióticas influyeron solo a escalas pequeñas. La altitud y la insolación provocaron divergencia funcional y filogenética en los Andes Mediterráneos de Chile, sin embargo, la interacción de estos dos factores produjo una convergencia funcional y filogenética. A pesar del acople de los dos tipos de diversidades la señal filogenética fueron menor que las esperada bajo un modelo de movimiento browniano de la evolución del rasgo. Por otro lado, encontramos discrepancias entre la diversidad funcional observada y esperada para algunos rasgos funcionales cuando se generaron comunidades aleatorias con probabilidades de ocurrencias de las especies en función de sus óptimos ambientales en el PN de Ordesa y Monte Perdido. Además, estas discrepancias se estructuraron a lo largo de distintos gradientes ambientales. Por último, cuando se compararon las relaciones entre los tres componentes de la diversidad (taxonómica, funcional y filogenética) y los factores abióticos y biótico, en zonas que difieren en clima e historia biogeográfica, se encontraron algunas relaciones más o menos constantes, pero la idiosincrasia fue el patrón predominante.

Conclusiones

La estructura de las comunidades de plantas alpinas subyace a las reglas ecológicas de ensamblaje, tanto bióticas y como abióticas. De este modo, los principales mecanismos que determinan la estructura de las comunidades de plantas de alta montaña en nuestras zonas de estudios son un complejo equilibrio entre competencia y facilitación producido en respuesta a la variabilidad en las condiciones ambientales, junto con el filtrado ambiental que producen las bajas temperaturas de alta montaña. En algunas ocasiones, a pesar de encontrar los mismos patrones de ensamblaje en regiones con distinto clima, los mecanismos responsables pueden diferir. En otras ocasiones las relaciones entre la comunidad y sus determinantes pueden ser totalmente idiosincráticos llegando a encontrar relaciones completamente opuestas. El efecto de los determinantes bióticos y abióticos en la diversidad taxonómica ve incrementada su intensidad a escalas espaciales específicas debido a que los procesos subyacentes al ensamblaje actúan a diferentes escalas espaciales. Por ejemplo, la altitud influye a la diversidad taxonómica a mayor escala que las interacciones bióticas, cuyo efecto se detecta a las escalas finas donde las interacciones entre plantas se dan.

Nuestros resultados sugieren que al menos en resoluciones espaciales pequeñas, las interacciones bióticas son un factor crítico del ensamblaje de las comunidades del centro de Pirineos, que dejan una huella detectable en la estructura funcional de rasgos como la altura máxima de la planta o el peso de las semillas. Así el uso de modelos nulos que representan la acción de reglas abióticas simulando comunidades a partir de constricciones ambientales abióticas presentan un gran potencial para evaluar el efecto de las interacciones bióticas, como la facilitación o la competencia. Además, considerar interacciones entre gradientes, ya sean aditivas o sinérgicas, pueden revelar nuevas perspectivas para los procesos de ensamblaje de las comunidades. Por ejemplo, la interacción entre la altitud y la insolación produce divergencia funcional y filogenética como resultado de las interacciones facilitadoras donde las condiciones son más estresantes. Por el contrario, cuando las condiciones son más suaves, el dominio de unas pocas especies que son más competitivas podría conducir a patrones de convergencia funcional.

Introducción

Uno de los mayores desafíos que se vienen planteando los científicos desde Darwin and Wallace es dilucidar cuáles son los procesos que originan y mantienen la diversidad biológica a lo largo de todo el planeta a todas las escalas espacio-temporales (Jaccard 1912; Connell 1978; Weiher and Keddy 1995; Ricklefs 2008). Las preguntas puestas sobre la mesa en las últimas décadas cubren un amplio abanico que va desde aquellas que tratan de esclarecer los procesos que determinan la variación de la biodiversidad a escalas regionales, las que se centran en la organización de las comunidades, hasta aquellas que se centran en desentrañar los mecanismos y las reglas de ensamblaje que conducen la coexistencia local de las especies a las escalas más pequeñas (Keddy 1992; Weiher et al. 1998; Cavieres et al. 2006; Grace et al. 2011; Götzenberger et al. 2012; Fine 2015). Ya a principios del siglo pasado algunos de los primeros ecólogos en preocuparse por estas cuestiones sugerían que las comunidades ecológicas no se ensamblan al azar, y ponían en valor la existencia de procesos deterministas (Clements 1916; Phillips 1931). Por el contrario, otras corrientes de pensamiento contrapuestas y coetáneas de las anteriores consideraban que las comunidades son simplemente conjuntos de especies fruto de procesos estocásticos (Gleason 1939).

A pesar de que durante las últimas décadas se han desarrollado múltiples teorías para explicar la estructuración de la comunidad desarrollando los marcos deterministas y estocásticos (Shipley and Keddy 1987; Hubbell 2001; Lortie et al. 2004), el debate sigue siendo tan polémico como lo fue hace casi un siglo. Si bien, en la actualidad la controversia se centra en dos diferentes enfoques teóricos (Tilman 2004; Leibold and Mcpeek 2006; Chase 2014; Li et al. 2015), la teoría de nicho ecológico que sería la heredera de la visión *clementsiana* y la teoría neutral de la biodiversidad que bebería del azar *gleasoniano*. El primero, de mayor tradición y peso histórico, se basa principalmente en las respuestas de las especies que forman la comunidad al ambiente tanto abiótico como biótico. De este modo, la diferenciación de nicho entre las especies explicaría la biodiversidad a diferentes escalas involucrando una gran cantidad de factores como los recursos edáficos, el climas y los competidores (MacArthur and Levins 1967; Chase and Leibold 2003). Por otro lado,

la teoría neutral de la biodiversidad sugiere que todas las especies son idénticas en su eficacia biológica o "*fitness*" de especie y en el efecto que tienen unas sobre otras (Hubbell 2001) y se basa en la capacidad de los organismos para dispersarse y alcanzar un lugar por puro azar. Bajo esta perspectiva, los eventos evolutivos y biogeográficos junto con los estocásticos tienen un papel central en la estructuración de las comunidades.

Recientemente, hemos comprendido que la organización de la diversidad es respuesta simultánea a procesos de los dos tipos (Escudero and Valladares 2016) y que la existencia de estas discrepancias teóricas como ya indicó Chase (2014) podrían ser en realidad una respuesta a los diferentes tamaños de las ventanas espaciales a las que la biodiversidad es evaluada. Así, cada día tenemos más claro que la escala de observación altera nuestra percepción de la importancia relativa de los procesos neutrales y de nicho. Por tanto, puesto que los patrones de diversidad y sus determinantes varían a diferentes escalas espaciales (Harmon and Harrison 2015), la respuesta a las preguntas relacionadas con el ensamblaje de comunidades, desde las realizadas por biogeógrafos hasta las de los ecólogos de comunidades interesadas en lo que ocurre individuo a individuo, implica la integración y la necesidad de aplicar un enfoque metodológico que permita el estudio simultáneo de un conjunto de escalas espaciales, desde distribuciones regionales resultado de complejos procesos históricos y evolutivos, hasta las escalas más pequeñas en las que las interacciones planta a planta son críticas (Harmon and Harrison 2015) (Ricklefs 1987; Holt 1993; McGill 2010a).

Llegados a este punto, y como se menciona arriba, el paradigma actual sugiere que el ensamblaje de las comunidades locales es el resultado de la existencia de un complejo equilibrio entre procesos deterministas y estocásticos que subyacen a ambas teorías (Chase et al. 2011; Vellend et al. 2014; Escudero and Valladares 2016) y cuya fuerza relativa e importancia varía a lo largo de las escalas espaciales y temporales (Ricklefs 1987; Levine 1992; McGill 2010a; Chase 2014). Por un lado, en marco teórico actual sugiere que los procesos ligados a las denominadas reglas filogeográficas, como los procesos biogeográficos y los eventos macro-evolutivos, son responsables de la configuración de los patrones de diversidad a grandes escalas, o lo que es lo mismo, son responsables de la formación del conjunto de especies,

riqueza, o "*pool*" regional de especies que será el sustrato sobre los que operarán procesos que actuarán a escalas más pequeñas (Zobel 1997; Chesson 2000; Ricklefs 2004; Chase and Myers 2011). En consecuencia, a escalas pequeñas, son los procesos ecológicos que subyacen a las denominadas reglas ecológicas de ensamblaje (Diamond 1975; Keddy 1992) junto con procesos estocásticos como la extinción aleatoria y la deriva ecológica, los que determinan la estructura final de las comunidades locales (Tilman 2004; Chase 2014). La introducción de la noción de reglas ecológicas es una aportación muy sugerente de Diamond (1975) quien sugiere tras observar patrones de coocurrencia la existencia de mecanismos predecibles que organizan la coexistencia de las especies en las comunidades. Es un concepto simple y fácil de entender que ha sido dotado de contenido a lo largo de los últimos 40 años. Las reglas ecológicas se dividen en las reglas de dispersión, las reglas abióticas y las reglas bióticas (Götzenberger et al. 2012). Así, la actual metáfora equipara conceptualmente a los procesos selectivos (no entenderlo como un proceso evolutivo) o reglas, con "*filtros*" que actuarían de forma jerárquica y a escalas cada vez más finas para imponer la estructura de la diversidad en el ensamblaje de las comunidades (Wilson 1999; Götzenberger et al. 2012; HilleRisLambers et al. 2012). Así y de una manera muy esquemática, el conjunto de especies que pueden existir en un lugar concreto sería determinado a partir de la riqueza regional en función de la limitación de la dispersión de las especies (*dispersal rules*). Posteriormente, las limitaciones que imponen el ambiente sobre las especies capaces de colonizar dicha localidad determinan la composición a escalas aún más pequeñas (*abiotic rules*). Y por último, a esas escalas donde las especies interactúan unas con otras se producen relaciones tanto positivas como negativas *(biotic rules)* que promueven o limitan la coexistencia de las especies (MacArthur and Levins 1967; Grime 1973).

No hay duda de que en las últimas décadas con la aparición de la ecología de comunidades basada en rasgos y la integración de la información filogenética se han experimentado grandes progresos en la construcción de lo que se ha denominado la Teoría de Coexistencia (HilleRisLambers et al. 2012). De esta forma, para identificar los procesos que gobiernan las comunidades hemos pasado de tener en cuenta básicamente la acumulación de información taxonómica, es decir, cuantificar el número de especies y las distribuciones de sus abundancias en el tiempo y en el espacio (p.e. Rosenzweig 1995; Willig et al. 2003), a considerar el papel de cada

especie en la comunidad en función de sus rasgos funcionales y sus relaciones evolutivas, entendiendo que las reglas de ensamblaje van a operar fundamentalmente a través de dichos atributos (Keddy 1992; Webb et al. 2002). De esta manera, se supera la idea poco realista de que todas las especies son ecológicamente equivalentes y evolutivamente independientes (Pavoine et al. 2010; Swenson 2011). En este sentido, cabe destacar la explosión de trabajos publicados en las dos últimas décadas que han utilizado la aproximación funcional y/o filogenética con la intención de esclarecer las reglas que rigen el ensamblaje de las comunidades en un elenco completo de ecosistemas y regiones biogeográficas (Webb et al. 2002; Lepš et al. 2006; Swenson et al. 2006; Kraft et al. 2007; Pillar and Duarte 2010; Mason et al. 2012).

Como comentaba arriba la ecología basada en rasgos funcionales se fundamenta en la idea de que las especies participan en la comunidad y responden a las presiones ecológicas selectivas en función de sus atributos funcionales (Cornwell and Ackerly 2009; Shipley et al. 2016). Estos atributos funcionales reflejan las estrategias ecológicas de las especies ya que están relacionadas con características morfológicas, fisiológicas y fenológicas de las especies que resultan claves para su desempeño en los hábitats que ocupan (Violle et al. 2007). Sin duda, estas características hacen de los rasgos funcionales una buena herramienta para responder preguntas relacionadas con la existencia y detección de las reglas de ensamblaje tanto bióticas como abióticas. Por ejemplo, la ecología funcional basada en rasgos permite detectar la existencia de una fuerza abiótica conocida como filtrado ambiental la cual impulsa la coexistencia de especies funcionalmente similares excluyendo las especies que no están dotadas de los rasgos necesarios para persistir en esas condiciones (Lavorel and Garnier 2002; Mayfield et al. 2009). Por otro lado, la competición tenderá a evitar la coexistencia de especies demasiado similares entre sí, desde un punto de vista funcional (MacArthur and Levins 1967; Chesson 2000). Una de las limitaciones que presenta la ecología funcional es que a menudo algunos rasgos que son importantes en el desempeño de la planta en la comunidad no son considerados por desconocimiento o por falta de recursos para medirlos o estimarlos. Por esta razón, la relación de parentesco entre especies se usa como una medida de similitud ecológica bajo la premisa de que las especies emparentadas estrechamente serán ecológica y funcionalmente más similares que los parientes más distantes (Webb et al.

2002; Losos 2008; Burns and Strauss 2011). Por tanto, aunque el uso de filogenias ha permitido inferir eventos históricos como la diversificación de especies (Davis et al. 2002; Hughes and Eastwood 2006), la cuantificación de la relación filogenética entre especies se ha usado en numerosas ocasiones para desentrañar los procesos ecológicos que gobiernan el ensamblaje de comunidades a escalas espacio-temporales pequeñas (Hardy 2008; Mayfield and Levine 2010; Le Bagousse-Pinguet et al. 2017).

Una de las metodologías más usadas y potentes para detectar reglas ecológicas de ensamblaje en conjunto con la aproximación funcional y filogenética (ambas se basan en las distancias de similitud entre especies) son los modelos nulos (Gotelli and Graves 1996). Este potente enfoque se basa en la comparación de la distribución observada de los rasgos funcionales (de la relación filogenética o de cualquier característica de la comunidad observada) con las distribuciones nulas generadas al imponer restricciones a la aleatorización para conservar solo ciertas características de los datos (Gotelli and Graves 1996; Ackerly and Cornwell 2007; Kraft et al. 2007; de Bello 2012). De esta manera, si las especies que forman la comunidad son más parecidas ecológicamente o están más emparentadas de lo que cabría esperar dado el modelo nulo, se pueden inferir procesos como el filtrado abiótico o la exclusión competitiva (Diaz et al. 1998). Por el contrario, una divergencia funcional o filogenética podría estar revelando la importancia de la diferenciación de nicho en la determinación del en el ensamblaje, o incluso de facilitación entre las especies que componen la comunidad (Valiente-Banuet and Verdú 2007; Kraft et al. 2008). Este último ejemplo, pone de manifiesto el problema que tiene esta aproximación, ya que la interpretación de los patrones generados bajo un modelo nulo, en ocasiones se hace complicada, ya que los mismos patrones pueden ser producidos por distintos mecanismos.

Pese a la potencia de los modelos nulos para dilucidar si los patrones observados son congruentes con lo que cabría esperar por azar, hay una gran cantidad de algoritmos y esquemas de aleatorización que dificultan su elección y la llegada de un consenso metodológico mediante el cual atajar las preguntas ecológicas que subyacen el ensamblaje de las comunidades (Ulrich and Gotelli 2013; Ulrich et al. 2017). Estos modelos varían desde aquellos que mantienen fija la frecuencia de ocurrencia de las especies hasta aquellos que fijan la riqueza de especies en las

comunidades (Gotelli 2000; Gotelli and Entsminger 2003). Sin embargo, estos modelos nulos tienen una capacidad reducida para detectar procesos ecológicos específicos (Gotelli and Ulrich 2012), y en numerosas ocasiones identificar si los mecanismos que producen los patrones son bióticos o abióticos se hace complicado (Kraft et al. 2015; Cadotte and Tucker 2017). En los últimos años, aunque se ha logrado progresar significativamente en el desarrollo de nuevas algoritmos con un sentido ecológico más profundo y claro (Peres-Neto et al. 2001; Cornwell et al. 2006; de Bello et al. 2012; Chalmandrier et al. 2013; Miller et al. 2017), se mantiene la necesidad de avanzar hacia el desarrollo de algoritmos que reproduzcan los patrones que cabría esperar si operasen reglas de ensamblaje o mecanismos concretos. De este modo, si no ocurren desviaciones de la configuración funcional (o filogenética) respecto a la configuración esperada bajo el modelo nulo con dichas características, quedaría reflejada la prevalencia del mecanismo (Gotelli and Ulrich 2012).

En este sentido, la alta montaña se presenta como un excelente sistema donde detectar de las reglas ecológicas de ensamblaje ya que las comunidades de plantas alpinas que allí viven están sometidas a una predecible variación en las condiciones ambientales en muy cortas distancias (Körner 2007; Sanders and Rahbek 2012). Así, pequeños cambios de altitud pueden significar grandes cambios en temperatura y humedad, pero también, variaciones en la distribución y duración del paquete de nieve o incluso longitud del período vegetativo en el cual las plantas pueden crecer y reproducirse (Körner 2003). Existen otros factores topográficos que son críticos en ambientes alpinos, como la pendiente o la orientación, y que también pueden generar diferencias microclimáticas, (Copeland and Harrison 2015). De hecho, uno de los patrones más ampliamente conocidos es el de la variación en la composición de especies que suele ocurrir en las distintas laderas de una montaña (Badano et al. 2005). Si bien, en la mayoría de los casos, el efecto que produce estos factores topográficos en la estructura de la vegetación tiene que ver con la incidencia de la radiación solar (Holland and Steyn 1975), en otros casos puede generar variación espacial en las propiedades del suelo (Yimer et al. 2006). Es precisamente la heterogeneidad ambiental relacionada con las propiedades del suelo otro importante estructurador de la diversidad de la vegetación que actúa a pequeñas escalas (Hutchings et al. 2009). En este sentido, especies en parches pobres pueden ver limitado su desarrollo e incluso su supervivencia, mientras que en parches ricos se

pueden desencadenar complejas interacciones de competencia (Theodose and Bowman 1997; Reynolds and Haubensak 2009). Sin ir más lejos, las interacciones bióticas juegan un papel clave en los procesos que gobiernan el ensamblaje de comunidades de plantas de alta montaña. Concretamente, la facilitación, cuya prevalencia tiende a aumentar con la severidad ambiental, y por tanto, con la altitud en los sistemas alpinos (Choler et al. 2001; Callaway et al. 2002; Cavieres et al. 2014).

No podemos dejar de indicar que a pesar de la severidad de los ambientes alpinos, y del efecto general que producen los gradientes de estrés asociados a las montañas en las comunidades de plantas, sus respuestas locales y los procesos subyacentes varían a lo largo de los distintos sistemas montañosos debido a características idiosincráticas y factores de gran escala como el clima o la historia evolutiva de las especies de la comunidad (Wiens and Donoghue 2004; Safi et al. 2011). Por ejemplo, la sequía estival propia del clima Mediterráneo puede ejercer un papel de filtro ambiental muy intenso condicionando la estructura y la composición de estas comunidades sobre todo a cotas más bajas (Giménez-Benavides et al. 2007; Mihoč et al. 2016). Por otro lado, los mismos determinantes podrían producir distintos patrones de diversidad en diferentes regiones que comparten clima, debido a que actúan sobre grupos de especies (*pools* florísticos regionales) con distintas características de partida. Sin duda alguna, el alto grado de idiosincrasia ecológica asociada a las distintas regiones se presenta como una limitación de las que hasta ahora ha adolecido la búsqueda de reglas ecológicas de ensamblaje.

En definitiva, aunque se ha realizado un gran esfuerzo en avanzar hacia un marco global para el ensamblaje de las comunidades, el éxito ha sido relativamente escaso (McGill 2010b; Chacón-Labella et al. 2016) y son muchas las discrepancias que se encuentran en la literatura cuando se tratan de encontrar las reglas de ensamblaje en determinadas comunidades o entre algunas muy parecidas. Nosotros pensamos que una de las principales limitaciones en el avance en este campo tiene que ver con el hecho de que las escalas espaciales a las que se han abordado estas cuestiones son muy diferentes y por tanto los resultados que se han obtenido pueden ser discrepantes. A esto hay que sumarle que los clásicos modelos nulos que se han utilizado para atajar las preguntas no son capaces de reproducir patrones esperables

tras la acción de determinados mecanismos o reglas, con lo cual separar los procesos que determinan los patrones encontrados puede ser una tarea imposible.

Conscientes de las limitaciones que restringen el progreso hacia una comprensión del ensamblaje de las comunidades, proponemos, primeramente, evaluar la estructura de la comunidad a diferentes escalas espaciales, dado que tanto los procesos ecológicos como los estocásticos pueden cambiar entre escalas (Levine 1992; McGill 2010a). Además, se hace necesaria la cuantificación del papel ecológico y del grado de parentesco filogenético de cada especie en la comunidad para contemplar los componentes funcional e histórico y así poder inferir las reglas de ensamblaje a partir de las estructuras funcional y filogenética que tienen las comunidades. Para ello, parece primordial la necesidad de ir más allá de la generación de modelos nulos que suponen que los requisitos ambientales de las especies son similares (Gotelli and Ulrich 2012; Blois et al. 2014), y construir modelos nulos que consideren la estructura ambiental de los sitios ocupados (recuperación de las reglas abióticas de ensamblaje) y el tipo de interacciones que prevalece entre las distintas especies (reglas bióticas de ensamblaje). Consciente de la importancia que tienen el contexto climático y evolutivo en el que están embebidas las comunidades y los procesos que determinan su estructura, hemos seleccionado dos regiones con historias evolutivas y biogeográficas completamente diferentes (Europa / Sudamérica) y dentro de cada región dos cordilleras con climas contrastados. Específicamente, en cada región biogeográfica se ha seleccionado una cordillera de clima mediterráneo, el sistema central de la península ibérica y los Andes centrales, así como una sometida a clima templado, la montaña ártico-alpina de Pirineos y la subantártica de los Andes meridionales. Pensamos que todo este planteamiento va a permitir desentrañar las reglas ecológicas de ensamblaje que organizan la coexistencia de las plantas en comunidades de alta montaña, o al menos, para ser más realistas, avanzar en este reto.

Objetivos

Nuestro objetivo es intentar arrojar luz en aquellos aspectos menos consolidados para una teoría global de coexistencia de especies de plantas, enfatizando la superación de las limitaciones expuestas anteriormente, e identificando las reglas ecológicas de ensamblaje que subyacen a los patrones de diversidad de las comunidades. Nuestra idea motora es que las variaciones idiosincráticas en la detección de las reglas de ensamblaje en tipos concretos de comunidades pueden ser explicados por cuestiones históricas y evolutivas. Para ello, nos basamos en el estudio de las comunidades de plantas de alta montaña, por ser un sistema muy rico en especies y cuyas peculiaridades ambientales hacen de él un modelo único para desentrañar los procesos deterministas que subyacen a las reglas ecológicas de ensamblaje y profundizar en la organización de estas reglas a través de las diferentes escalas espaciales. Concretamente el planteamiento adoptado en esta tesis nos permitirá conocer cómo el efecto de las variaciones ambientales a pequeña escala interactúa con las condiciones climáticas y con la historia biogeográfica del territorio. En este sentido, las comunidades de alta montaña son muy parecidas estructuralmente, independientemente de la historia biogeográfica que ha determinado el pool florístico regional en cada una de ellas. Si además estudiamos dentro de cada región biogeográfica, montañas con climas muy contratados (en nuestro caso climas mediterráneos frente a otros templados) podemos aislar algunos de los factores ambientales que pueden determinar los ensamblajes locales. Para enfrentarnos a este objetivo general hemos abordado los siguientes objetivos específicos:

- Analizar la variación de la diversidad taxonómica en comunidades de plantas de alta montaña (incluyendo la diversidad alfa y la beta) a lo largo de diferentes gradientes altitudinales situados en latitudes contrastadas de los Andes chilenos. Y determinar el grado en el que factores abióticos (la radiación solar y la heterogeneidad del suelo) y bióticos (interacciones entre especies) modulan los efectos de la latitud y la altitud identificando la escala espacial a la que se acentúan sus efectos. Los Andes chilenos representan un modelo ideal para estudiar la variación en estas comunidades dado que su disposición norte-sur ha permitido que las

especies se desplacen durante los avatares climáticos homogenizando el pool florístico.

- Cuantificar la dispersión filogenética y funcional a lo largo de múltiples gradientes abióticos en las comunidades de plantas alpinas en los Andes Mediterráneos de Chile y evaluar la señal filogenética en los rasgos funcionales para esclarecer el grado en que la diversidad filogenética proporciona distinta información a la suministrada por la diversidad funcional. Las montañas Mediterráneas como las del centro de Chile presentan una fuerte sequía durante la época estival que se acentúa a bajas altitudes. Esta sequía se comporta como un filtro ambiental el cual podría afectar a la estructura funcional y filogenética.

- Detectar las reglas ecológicas de ensamblaje en las comunidades de plantas alpinas de los Pirineos Centrales generando modelos nulos que reproduzcan la estructura funcional que cabría esperar si operasen las reglas abióticas y bióticas. La vegetación de los Pirineos Centrales presenta una zonación de la vegetación muy marcada que sugiere la prevalencia de los procesos deterministas, y esto convierte a estas montañas en un buen modelo para encontrar las reglas ecológicas de ensamblaje.

- Explorar el efecto de los determinantes ambientales (elevación, nitrógeno total en el suelo, radiación solar y las interacciones bióticas) en la relación existente entre las diversidades taxonómica, funcional y filogenética mediante un modelo de ecuaciones estructurales, y comprobar si las relaciones en este complejo entramado son generales, o inherentes a las condiciones climáticas y la historia evolutiva por la cual se forman la riqueza de especies regional de las cuales se forman las comunidades locales.

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Capítulo 1

Determinants of high mountain plant diversity in the Chilean Andes: from regional to local spatial scales

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Abstract

Mountains are considered excellent natural laboratories for studying the determinants of plant diversity at contrasting spatial scales. To gain insights into how plant diversity is structured at different spatial scales, we surveyed high mountain plant communities in the Chilean Andes along elevational gradients located at different latitudes taking into account factors that act at local and fine scales, including abiotic (potential solar radiation and soil quality) and biotic (species interactions) factors, and considering multiple spatial. Species richness, inverse of Simpson's concentration (D_{equiv}), beta-diversity and plant cover were estimated using the percentage of cover per species recorded in 34 sites. Overall, plant species richness, D_{equiv} and plant cover were lower in sites located at higher latitudes. We found a unimodal relationship between species richness and elevation and this pattern was constant along the three massifs independently of the regional climatic conditions. Soil quality decreased the beta-diversity among the plots in each massif and increased the species richness, the D_{equiv} and cover. Segregated patterns of species co-occurrence were related to increases in species richness, D_{equiv} and plant cover at fine scales. Our results demonstrate that elevational patterns of plant diversity remained constant along the regions although the mechanisms underlying these diversity patterns may differ among climatic regions. Our results show that the patterns of plant diversity in alpine ecosystems respond to a series of factors (abiotic and biotic) that act jointly at different spatial scale determining the assemblages of local communities, but their importance can only be assessed using a multi-scale spatial approach.

Keywords: Alpine ecosystem; Beta-diversity; Community assembly; Ecological gradients; Species interactions; Summer drought

Introduction

Mountains are considered excellent natural laboratories for investigating how plant diversity is structured at contrasting spatial scales because their extreme environmental conditions and the steep climatic gradients over short distances suggest that deterministic processes become prevalent in community assembly (Körner 2007; Sanders and Rahbek 2012). For instance, at regional scales, the most frequently observed pattern is a decreasing trend in species richness with elevation (Rahbek 1995; Rosenzweig 1995; Körner 2007; Cuesta et al. 2017), explained by a combination of factors such as increasing environmental harshness and decreasing area available for colonization with elevation (Grytnes 2003; Körner 2007). However, this diversity pattern sometimes changes to a hump-backed relationship where species richness peaks at medium elevations (Rahbek 1995; Grytnes 2003; Nogués-Bravo et al. 2008). This variation is related to the fact that some gradients are very long with dramatic changes in the vegetation types along them (high turnover rates along elevation within mountain ranges: Grytnes 2003), due to the historical human footprint and disturbances (Billings 1973; Olff and Ritchie 1998), or simply because the diversity patterns are compared at different spatial scale (Götzenberger et al. 2012).

Factors operating at lower spatial scales may influence or alter patterns observed at larger spatial scales. For instance, at local (medium) spatial scales in high elevations where temperatures are very low, environmental variations such as those induced by solar radiation may yield milder conditions due to an early snowmelt and an increase in the length of the effective growing season, which is beneficial for alpine plants (Körner 2003). In addition, at a local scale, soil quality that allow greater

primary productivity and plant diversity regardless of the overall habitat quality, could affect the expected patterns of elevational decrease in species richness.

In addition, biotic interactions such as competition and facilitation are critical determinants of plant diversity at the finest spatial scales in many ecosystems (Callaway 2007; Luzuriaga et al. 2011), including alpine plant communities (Choler et al. 2001; Cavieres and Badano 2009; Cavieres et al. 2014; Pescador et al. 2014). In particular, competition in benign environments (i.e. low elevation) promotes richness by niche differentiation but with dominance by a reduced group of species due to competitive exclusion. When environmental conditions become more stressful with elevation, facilitative interactions become more important (Callaway et al. 2002; Michalet et al. 2006) and it has been shown that they can dampen the decreases in species richness acting as safety-net under stressful conditions (Cavieres et al. 2016). Thus, at fine spatial scale we might not expect a monotonic decrease in diversity with elevation.

The Chilean Andes comprise a continuous and large north to south system of mountain massifs, and thus the effects of environmental gradients on plant community richness can be studied at multiple scales. Furthermore, in contrast to other mountainous areas where the landscape and biota have been profoundly altered by human activities (Schwörer et al. 2015), thereby hindering the interpretation of diversity patterns (Billings 1973; Olff and Ritchie 1998), the Chilean Andes are characterized by a very low level of human-driven disturbances, especially in the southern region (Huber and Markgraf 2003). In addition, there are clear climate variations over a broad regional scale and it is possible to discern major differences along this mountain range.

To gain insights into how plant diversity is structured at different spatial scales -plot (20 x 20m), subplot (2.4 x 2.4 m) and cell (30 x 30 cm)- in the Chilean Andes, we surveyed plant communities along an elevational gradient at different latitudes (from –32°S to –52°S) comprising mountains with a Mediterranean-type climate where the summer drought is critical (Cavieres et al. 2006) to sub-Antarctic mountains where summer drought is negligible but summer temperature is low. Our main objectives were: (i) to determine the effect of elevation on taxonomic plant diversity (including alpha diversity as well as beta-diversity) and productivity (plant cover) at different spatial scales including some contrasted latitudes along the Chilean Andes; and (ii) to determine whether factors that act at local and fine scales, including abiotic (potential solar radiation and soil quality) and biotic factors (species interactions), might modulate the effects of latitude and elevation on different components of plant diversity. We expected taxonomic diversity and productivity to decrease with elevation, but a mid-elevational peak was expected in mountains with a Mediterranean-type climate due to the effect of the summer drought at lower elevations (Cavieres et al. 2006).

Materials and methods

Study area

We selected three high mountain massifs over a long latitudinal gradient in the Chilean Andes (see Table 1, Fig. 1): (1) Farellones located 40 km east of the city of Santiago; (2) Maule situated 100 km east of the city of Talca; and (3) Torres del Paine National Park located in sub-Antarctic Patagonia at 75 km north of the city of Puerto Natales. Farellones and Maule are influenced by a Mediterranean-type climate, where the summer drought is more pronounced at lower elevations, although the duration

and the effect are greater in Farellones than in Maule. Torres del Paine has a sub-Antarctic climate without summer drought where the rainfall is distributed evenly throughout the ***Table 1*** *Geographic location, main climatic characteristics, treeline altitude, and treeline species for the study sites*

Study site	Location	Treeline altitude (m.a.s.l.)	Annual precipitation (mm)	Mean temperature (°C)	Treeline species
Farellones	33°2′S, 70°1′W	2200	943[1]	6.5[2]	*Kageneckia angustifolia* (Rosaceae)
Maule	35°6′S, 70°3′W	1700	900[3]	5[3]	*Nothofagus antarctica* (Nothofagaceae) and *Austrocedrus chilensis* (Cupressaceae)
Torres del Paine	51°0′S, 73°0′W	500	900[4]	5[4]	*Nothofagus pumilio* (Nothofagaceae)

In these areas, the precipitation occurs mainly as snow during the winter. Climatic data for each region are shown in Table 1.

Above the treeline, alpine vegetation ranges from 2477 to 3627 m in Farellones, from 2064 to 2666 m in Maule, and from 500 to 1050 m in Torres del Paine. The vegetation in these mountains is generally dominated by caespitose herbs, which are accompanied by other growth forms such as prostrate shrubs (e.g., *Berberis empetrifolia* Lam.), perennial forbs (e.g., *Phacelia secunda* J.F. Gmel. and *Nassauvia pyramidalis* Meyen), and cushion-like plants (e.g., *Azorella madreporica* Clos and *Laretia acaulis* (Cav.) Gillies & Hook). The treelines are formed by *Nothofagus*

pumilio (Poepp & Endl.) (Notophagaceae) Krasser in Torres del Paine National Park, *Austrocedrus chilensis* (Cupressaceae) in the Maule mountain, and *Kageneckia angustifolia* D. Don (Rosaceae) in Farallones (see Table 1).

Field sampling

Field sampling was performed in the Mediterranean and sub-Antarctic climate regions during the summer in 2014 and 2015, respectively, when the alpine plants were at their phenological peak. We sampled a total of 34 sites (11 in Farellones, 9 in Maule, and 14 in Torres del Paine) in order to capture the local variability in alpine-type vegetation by considering a wide range of elevations, aspects, and slopes. At each site, the vegetation was surveyed at three different scales: (1) plot scale: one 20 m × 20 m sampling plot was established at each of the 34 sites; (2) quadrat scale: five 2.4 m × 2.4 m quadrats were established within each plot, with one in each corner and a fifth in the centre to form 170 quadrats; and (3) cell scale: the central quadrat was divided into 64 cells measuring 30 cm × 30 cm, with a total of 2176 cells (Fig. 1). The percentage cover per species was sampled in each quadrat and in each cell. The plant cover per plot was calculated indirectly as the sum of the mean cover of each species in the five quadrats, where the plant cover in the central quadrat was estimated as the mean cover by each species in the 64 cells.

The cell data information obtained at the finest scale was used to estimate the checkerboard score (C-score: Stone and Roberts 1990), which quantifies the degree of spatial segregation for species co-occurrence, as an integrative estimate of plant to plant interactions. High C-score values denote that species pairs occur less frequently whereas low values indicate a tendency for species to aggregate spatially. The average

size of the plant species in the community was around 15 cm in diameter, so the cell size appeared to be adequate for estimating real biotic interactions.

The environment at each site was characterized by measuring several variables. In particular, elevation and aspect were obtained using a GPS (Garmin Colorado-300, Garmin Ltd, Olathe, USA), and slope with a clinometer (Silva Clinomaster, Silva Sweden, Sollentuna, Sweden). Elevation was standardized among the different massifs in order to compare regions at various latitudes by subtracting the mean treeline elevation (determined using Google Earth images) from the plot elevation. Aspect and slope values were used to calculate Gandullo's potential solar radiation coefficient (Gandullo 1974).

In addition, to assess the overall quality of the sampled unit, two soil cores with a diameter of 5 cm and depth of 10 cm were collected from each corner-quadrat, with one from an open area and the other under the perennial and dominant vegetation, thereby yielding eight soil samples per plot. The soil samples were air dried for one month and then sieved through a 2-mm mesh. We assessed eight multi-functional ecosystem properties related to the cycling and storage of nutrients. In particular, we selected organic carbon (C), total nitrogen (N), available phosphorus (P), and potassium (K) as key nutrients related to primary productivity and the buildup of nutrient pools (Maestre et al. 2009). These parameters are also surrogates for other forms of C, N, and P that are available to plants (Delgado-Baquerizo et al. 2013), and they can be treated as ecosystem functions related to soil fertility and primary productivity. Furthermore, we estimated the enzymatic activities of phosphatase and β-glucosidase, which are closely related to the microbial functionality and nutrient dynamics in soil. Soil organic C was determined by

colorimetry after oxidation with a mixture of potassium dichromate and sulfuric acid (Yeomans and Bremner 1988). Total N and available P were determined with a SKALAR++ San Analyzer (Skalar, Breda, The Netherlands) in our laboratory after digestion with sulfuric acid and Kjedahl's catalyst (Anderson and Ingram 1994). Potassium (K) was measured with the same analyzer system after shaking the soil samples with distilled water (1:5 ratio) for 1 h. Enzymatic activities were estimated using the methods described by Eivazi and Tabatabai (1988; β-glucosidase) and Tabatabai and Bremner (1969; acid phosphatase). The soil pH and electrical conductivity were measured in a soil and water suspension at a mass:volume ratio of 1:3 using a pH meter (GLP 21; Crison, Barcelona, Spain) and a conductivity meter (GLP 31; Crison, Barcelona, Spain), respectively. These variables were then averaged to obtain quadrat-level estimates based on the mean values determined in bare ground and vegetated areas, where they were weighted by the respective cover value in each quadrat. The centre quadrat value was estimated as the average of the four quadrats at each site. All of these soil variables are determinants of the functioning of ecosystems (Reiss et al. 2009; Jax 2010), so we calculated an ecosystem multi-functionality index (Maestre et al. 2012):

$$M_i = \left(\sum_{k=1}^{n} (x_{ki} - \mu_k)/\sigma_k \right) /n,$$

where M_i is the multi-functionality of plot i, n is the total number of soil parameters, x_{ki} is the value of parameter k in plot i, and μ_k and σ_k are the mean and standard deviation for each parameter k, respectively.

Diversity metrics

Species richness (S) was estimated as the number of plant species recorded in each sample. We estimated the inverse of Simpson's concentration index (D_{equiv})

expressed as species richness equivalents as an additional alpha diversity measure according to Jost (2007):

$$D_{equiv} = 1/\sum_i^S p_i^2,$$

where p_i is the cover proportion of species i and S is species richness. Cover data were square root-transformed before estimating the inverse of Simpson's concentration index and the beta-diversity.

We also measured beta-diversity to assess the non-directional variation in species composition across sampling units (Anderson et al. 2011). We calculated beta-diversity as the mean pairwise Bray–Curtis floristic dissimilarities among samples (i.e., cells, quadrats and plots) within each group depending on the spatial scale (Anderson et al. 2011):

$$\bar{d} = \frac{1}{n-1}\sum_{i,j<i} d_{ij},$$

where n is the number of samples within each group and d_{ij} is the dissimilarity of a target sample *i* relative to another sample *j*. Thus, *plot beta-diversity* was the mean of all the pairwise dissimilarities between a target plot and the other plots within each of the three mountainous massifs. *Quadrat beta-diversity* was the mean of all the pairwise dissimilarities between a target quadrat and the other four quadrats within each of the 34 plots. *Cell beta-diversity* was the mean of all the pairwise dissimilarities between a target cell and the other 63 cells within each of the 34 centre quadrats.

Finally, we measured plant cover (C, estimated as the sum of the cover by all species because the level of overlapping was very low in these plant communities) in each sampling unit as a surrogate for productivity.

Statistical analyses

The relationships between the standardized elevation, soil quality assessed by soil multi-functionality, potential solar radiation, biotic interactions (C-score), and species richness were analysed using generalized linear models (GLMs) at the plot scale, and with generalized linear mixed-effects models (GLMMs) at the quadrat and cell scales. A Poisson error distribution and logarithmic link function were selected in both cases. The inverse of Simpson's concentration index, beta-diversity, and total plant cover were analysed with linear models (LMs) at the plot scale, and with linear mixed-effects models (LMMs) at the quadrat and cell scales using a Gaussian error distribution and identity link function. We included region (i.e., Farellones, Maule, and Paine) as a fixed factor and plot as a random factor. Post hoc Tukey tests were performed to detect any significant differences among regions. The convenience of including the quadratic term of elevation and the interaction between elevation and massifs in the final models was evaluated using the AICc criterion. We checked for collinearity between the different environmental predictors using the variance inflation factor before implementing the models where they were below 2 in all cases, thereby indicating the absence of problems with co-linearity (Chatterjee and Hadi 2001). The normality of the standardized residuals was confirmed visually for all of the models. We square root-transformed the total plant cover in order to normalize the data before conducting the analyses. We estimated the statistical significance of each predictor using type-II analysis of variance. We calculated the total variance explained (R^2) by each LM and GLM, and the conditional variance explained (R^2_c) by both fixed and random factors, as well as the marginal variance explained (R^2_m) by fixed factors for each LMM and GLMM using the MuMIn package. All of the

statistical analyses were performed in R using the lme4, car, and vegan packages (v 3.2.4; R Core Team 2016).

Results

We recorded a total of 234 perennial plant species (a list of taxa are provided in Online Resource 1) in the 34 plots sampled in the three regions, with a total of 86, 86, and 118 species in the Farellones, Maule, and Torres del Paine NP, respectively. The species richness ranged from 12 to 50 species per plot, with a mean of 25.3 ($\pm$ 10) plant species per plot (other mean of diversity metrics on three regions at three scales are provided in Online Resource 2). The most abundant species in Farellones were the cushion plants *Azorella madreporica* and *Laretia acaulis*, and graminoids such as *Rytidosperma pictum* and *Poa cf. denudata*. The graminoids comprising *Festuca acanthophylla* and *Poa* cf. *denudata* were dominant in the Maule region. Finally, in the sub-Antarctic region, the community was dominated by prostrate shrubs such as *Empetrum rubrum* at low elevations, whereas the higher zones were dominated by the cushion plant *Azorella monantha*.

The fitted models explained a high proportion of the variance in the diversity component at all of the spatial scales considered (Table 2). There were significant relationships between all of the diversity metrics (i.e., species richness, inverse of Simpson's concentration index or equivalent richness, beta-diversity, and total plant cover) and some of the predictors.

Effects of elevation

At plot scale, the quadratic relationship between elevation and species richness significantly improved goodness of fit compared to a linear model (AICc with quadratic term = 246.2 vs. without = 251.6). In addition, a more complex model

including the interaction between elevation and massifs produced lower goodness of fit for all diversity metrics and scales. The negative quadratic relationship between elevation and species richness (Table 2) indicated that the number of species was higher toward intermediate elevations above the local treeline (500–700 m standardized elevation) with a decrease toward both edges, which was more pronounced toward the upper limit (summits). This pattern was observed across the different latitudes despite species richness differed among regions, being significantly higher in Torres del Paine than in Farellones (Table 2). Plant cover was negatively influenced by elevation at large scales (plot and quadrat scales; see Table 2), and plots in Torres del Paine had significantly higher plant cover than in Farellones at plot scale. The inverse of Simpson's concentration index showed no statistically significant relationship with elevation. However, this index was significantly lower in Farellones than in the other two sites and the differences in the inverse of Simpson's concentration index among regions were consistent at the three spatial scales considered (Table 2). Lastly, the beta-diversity exhibited a strong monotonic decrease with elevation at the plot scale but not at finer scales (Table 2). The dissimilarity of the species composition (beta-diversity) among plots in each massif was significantly lower in Torres del Paine than in Farellones (Table 2).

Table 2 Coefficients of the models (GLM, LMs, GLMM and LMMs) examining the effects of environmental factors on the diversity indices at plot (20 x 20 m), and at quadrat (2.4 x 2.4 m) and cell (30 x 30 cm) scales

	plot scale		quadrat scale		cell scale	
Species richness						
Intercept (Farellones)	3.08		2.27		0.48	
Massif		**		**		**
Maule	0.24	ab	0.26	ab	0.63	ab
Torres del Paine	0.29	b	0.43	b	0.63	b
Altitude	-0.12	**	-0.08		-0.02	
Altitude^2	-0.10	**				

Soil quality	0.20	***	0.14	**	0.32	**
Potential solar radiation	0.02		0.04		0.07	
C-score	0.07		0.19	***	0.45	***
R^2	0.89					
R^2m			0.39		0.41	
R^2c			0.70		0.56	

Inverse of Simpson's concentration

Intercept (Farellones)	6.21		4.91		1.20	
Massif		**		**		***
Maule	9.50	b	3.47	ab	1.55	b
Torres del Paine	9.12	b	4.62	b	1.52	b
Altitude	-0.16		0.06		0.17	
Soil quality	3.80	*	0.99	*	0.69	**
Potential solar radiation	0.07		0.29		0.03	
C-score	1.32		1.88	**	1.01	***
R^2	0.50					
R^2m			0.32		0.38	
R^2c			0.67		0.53	

Beta-diversity

Intercept (Farellones)	0.86		0.48		0.78	
Massif		***				
Maule	-0.05	a	-0.01		0.04	
Torres del Paine	-0.16	b	0.05		0.01	
Altitude	-0.04	**	0.03		0.00	
Soil quality	-0.04	*	-0.00		-0.01	
Potential solar radiation	0.01		-0.01		-0.03	
C-score	-0.01		0.03		-0.06	
R^2	0.67					
R^2m			0.18		0.16	
R^2c			0.64		0.63	

Plant cover

Intercept (Farellones)	14.134		2.634		2.16	
Massif		*				
Maule	7.599	ab	-0.065		0.17	
Torres del Paine	15.836	b	0.242		-0.07	
Altitude	-2.825	*	-0.239	*	0.03	
Soil quality	9.081	**	0.286	*	0.43	*
Potential solar radiation	1.649		0.051		0.20	
C-score	2.849		0.197	*	0.32	*

R^2	0.62		
R^2m		0.25	0.17
R^2c		0.39	0.33

Altitude^2: the quadratic term of altitude.

R^2: variance explained by each model. R^2m: marginal variance explained by fixed factors. R^2c: conditional variance explained by both fixed and random factors.

The significance is shown as *** $P<0.001$, ** $P<0.005$, * $P<0.05$.

Different letters within columns indicate significant differences ($P< 0.05$) between Farellones (a) and the other two regions according to Tukey's range test

Effects of local abiotic environment

We detected that soil quality correlated positively with plant assemblages with higher species richness, the inverse of Simpson's concentration index, and total plant cover; these relationships were maintained across the three spatial scales (Table 2). The beta-diversity decreased as soil quality increased at the plot scale (Table 2). There were no significant relationships between the diversity metrics and solar potential solar radiation (Table 2).

Effects of species interactions

In general, the C-score index was positively associated with all the diversity metrics at fine spatial scales. The species richness, inverse of Simpson's concentration index, and plant cover increased as the frequency of species co-occurrence decreased at the quadrat and cell scales. Thus, a shift from an aggregated to segregated species co-occurrence pattern was observed with the increase in the number of species, the inverse of Simpson's concentration index, and plant cover (Table 2). In addition, species segregation was associated with decreases in the mean pairwise dissimilarities (beta-diversity) between cells.

Discussion

The results of the present study showed that the patterns of plant diversity in alpine ecosystems respond to a series of factors that act at different spatial scale, i.e. climatic variation related to latitude, local variations in elevation and potential solar radiation, small scale variations in soil quality, and fine scale species interactions. Our results support the idea that the general variation of the elevational pattern in plant diversity can be due to the effect exerted by other concomitant factors which are able to modify the primary patterns (Billings 1973; Rahbek 1995; Olff and Ritchie 1998; Grytnes 2003; Nogués-Bravo et al. 2008).

We found that species richness exhibited a unimodal relationship with standardized elevation, with the maximum values at medium elevations within massifs and the minimum values at both edges of the gradient. Surprisingly, this pattern was constant along the three massifs and it was independent of the regional climatic conditions. The expected pronounced decrease in richness (and productivity) is due to the environmental severity (Rahbek 1995; Grytnes 2003), which increases with elevation because of coldness, short growing seasons, excessive radiation, and other factors (Körner 2007). This would induce a monotonic relationship, which is then modulated by other local factors to obtain a unimodal pattern. In our opinion, the factors responsible for generating this humped pattern differed among regions and climates. For instance, high mountain Mediterranean-type massifs are characterized by summer drought at low elevations, which shortens the growing season (Cavieres et al. 2006). This implies that stress is intense at both ends of the elevational gradient with coldness at the highest elevations and drought at the lowest elevations, but more benign conditions at intermediate elevations (Mihoč et al. 2016) and therefore greater species richness. Some previous studies have suggested that water deficit is not a critical determinant of plant diversity in alpine habitats (Körner 2007) but our results

agree with those obtained in Mediterranean regions (Cavieres et al. 2006; Giménez-Benavides et al. 2007; Reverter et al. 2010).

In the temperate Chilean Andes, particularly in the sub-Antarctic regions, summer drought is practically negligible, thus the humped pattern in species richness along elevational gradient observed in the sub-Antarctic Patagonian Andes may be related to other mechanisms. The existence of hard boundaries at both ends of the elevational gradient (Grytnes and Vetaas 2002), mass effect in an ecotone zone (Grytnes 2003), or higher intensity competitive exclusion at low elevations (Grime 1973; Bruun et al. 2006) and a disturbance regime (e.g. higher grazing intensity at low elevation: Grytnes et al. 2006) are factors that have been claimed to explain this pattern in other sub-Arctic mountains. However, we consider that the diversity pattern observed in Patagonian Andes is probably attributable to the existence of positive plant–plant interactions at intermediate elevations. It is known that facilitation by cushion plants and other nurse plants that dominate alpine ecosystems increases species richness at the entire community level (Cavieres and Badano 2009). Many studies have also shown that the magnitude of facilitation increases with the stress level (i.e., elevation), which could led to an increase in richness as elevation increases (Cavieres et al. 2002; Callaway et al. 2002; Arroyo et al. 2003). Nonetheless, the intensity of the facilitative effect declines under extremely stressful conditions (Michalet et al. 2006), and thus a decay in species richness is expected at the uppermost limit of the elevational gradient. As a consequence, different mechanisms can probably generate very similar humpback patterns under contrasting climates and independently of the net differences in species richness along the mountain range (Fig. 2).

The importance of biotic interactions was also supported by the associations between the C-score and plant diversity and productivity (i.e., total plant cover) in the assemblages at the quadrat and cell spatial scales. We found that species segregation was related to higher species richness, diversity, and total plant cover, thereby suggesting spatial repulsion of species to avoid or reduce competition (MacArthur and Levins 1967; Chesson 2000; Silvertown 2004), which allowed more species to co-occur. However, the species co-occurrence patterns were not related to any of the plant diversity metrics at the plot scale. Therefore, the effects of species interactions could only be detected when we considered the community in detail, specifically at the spatial scale comprising the neighbourhoods of plants with which they could potentially interact.

An increase in environmental severity with elevation was also strongly supported by the decrease in beta-diversity with elevation at the local scales in the assemblages that we surveyed, where the species compositions of the plant communities became more similar as elevation increased within the massifs. Other studies performed along elevational gradients also found a decrease in beta-diversity toward high elevations (Vázquez and Givnish 1998; Wang et al. 2002; Kraft et al. 2011). Our results may be attributed to harsh conditions acting as abiotic filters, thereby reducing the available species pool and leading to more homogeneous plant assemblages. In addition, soil quality that relates to critical ecosystem functions, such as carbon storage, productivity, and the buildup of nutrient pools (Maestre et al. 2012), decreased the compositional dissimilarity among plots in each massif. The differences in beta-diversity among communities found here may have been related to the dominance of prostrate nurses and cushion-like shrubs such as *Azorella madreporica* and *Empetrum rubrum*. These species enhance soil quality because they

increase the availability of nutrients under their canopies (Jones et al. 1994; Badano and Cavieres 2006; Mihoč et al. 2016) generating fertility islands (Escudero et al. 2004; Badano and Cavieres 2006). This implies that nurse species produce improvements of soil quality and amelioration of the extreme environmental conditions generating more stable and predictable conditions compared to the surrounding environment areas leading to species rich and constant assemblies, resulting in a decrease in beta-diversity among plots (Kikvidze et al. 2015).

Our findings demonstrate that a multi-scale approach is necessary to elucidate the mechanisms that shape alpine plant diversity over a large area. The variations at the plot, quadrat, and cell scales remained constant for most of the factors, but the intensity of some factors appeared to be greater at specific scales. For example, elevation influenced the number of species and plant productivity, where these effects were clearly detectable at the plot scale, whereas the C-score was only affected at the finest (quadrat and cell) scales. Our results showed that the patterns of taxonomic diversity in alpine ecosystems are related to both large-scale variables (climate estimated indirectly based on elevation and latitude) and fine-scale variables (soil quality and biotic interactions), which jointly determine the assemblages of local communities. In addition, our results demonstrated that the patterns of taxonomic diversity with elevation remain constant along the regions in the Andes, although the mechanisms responsible for causing and maintaining these diversity patterns may differ among regions. The summer drought has important effects on the Andean communities in the central Mediterranean-type climate region of Chile (Cavieres et al. 2007; Giménez-Benavides et al. 2007) whereas facilitation may be critical in other regions. The combined effects of local biotic processes (such as facilitation) acting

over large-scale abiotic gradients as well as regional factors determine the community assembly and the overall diversity patterns in stressed ecosystems.

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Capítulo 2

Interactions between abiotic gradients determine functional and phylogenetic diversity patterns in Mediterranean-type climate mountains in the Andes

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Abstract

Questions: How do phylogenetic and functional trait dispersions respond to multiple abiotic gradients? Are functional trait and phylogenetic dispersions coupled across different spatial scales? Does phylogenetic signal on functional trait data help to elucidate the degree to which phylogenetic information is providing novel information?

Location: The study was performed in three massifs of the Mediterranean-type climate zone of the high Andes of central Chile.

Methods: We sampled plant species composition in 20 alpine sites above the treeline at three different spatial scales: plot (20 x 20m), subplot (2.4 x 2.4 m) and cell (30 x 30 cm). Functional and phylogenetic mean pairwise distances (MPD) calculated using data on six functional traits (maximum plant height, plant size, leaf area, specific leaf area, leaf dry matter content and leaf thickness) and a molecular phylogeny (rbcL and matK) were compared to the patterns expected under a null model to characterize the functional and phylogenetic dispersion along interacting elevation and potential solar radiation gradients.

Results: Our results show that functional and phylogenetic dispersion were related and influenced by potential solar radiation, but the effect of this factor varied with elevation. Overdispersion was found in the most stressful sites while clustering was observed where the conditions were milder, suggesting a relevant role of facilitation and competitive interactions, respectively. While Blomberg's K statistic indicated no phylogenetic signal for the studied plant traits, Pagel's λ indicated phylogenetic signal, but not of strong intensity (< 1), suggesting that the correlation between the functional and phylogenetic diversities was low and that additional unmeasured traits

with phylogenetic signal were likely to be important in determining the structure of the studied communities.

Conclusions: Our results support the hypothesis that biotic interactions modulated by environmental conditions are important for alpine plant community assembly. Moreover, they reinforce the notion that multiple processes shape community structure, and this can be elucidated by examining interacting environmental gradients such as elevation and potential solar radiation, and taking into account multiple spatial scales. Our results reinforces the use of both functional and phylogenetic diversities simultaneously and discourages the use of the phylogenetic diversity as a surrogate of the functional structure.

Introduction

Disentangling the drivers that determine community assembly and diversity patterns remains a critical topic in ecology (Lortie et al. 2004; Götzenberger et al. 2012; HilleRisLambers et al. 2012). The current paradigm suggests the existence of a complex balance between stochastic and deterministic processes (Chase et al. 2011) leaving detectable spatial signals on community properties (McIntire & Fajardo 2009; Pavoine et al. 2011). Species interactions (both positive and negative) and environmental filtering are considered the most relevant deterministic drivers of community assembly leaving observable imprints on the spatial structure (Wang et al. 2015; Chacón-Labella et al. 2016).

Critical for an appropriate understanding of the balance between deterministic and stochastic processes in community assembly is our ability to quantify the similarity of species, or the role played by each species, in the assembly process. The unrealistic assumption that all species are equivalent independently of the role that each of them plays in the field implicitly used when evaluating patterns of taxonomic diversity, has led to the evaluation of the functional similarity among species and their phylogenetic relatedness (Kraft et al. 2007; Cadotte et al. 2009) as indicators of the overall ecological similarity among species. For instance, the functional approach infer assembly processes by comparing the distribution of plant functional traits within communities with those expected from null assemblages. There, abiotic filtering and competitive exclusion lead to clustering of functional traits compared to null models (Diaz et al. 1998). Conversely, niche differentiation and facilitative interactions produce an overdispersion of functional traits (Valiente-Banuet & Verdú 2007; Kraft et al. 2008).

Although trait-based plant community ecology offers a valuable conceptual framework (Shipley et al. 2016) and the number of papers published using this approach has grown exponentially (Escudero & Valladares 2016), there are some limitations. One of these limitations is the reduced set of traits that are often measured. Sometimes, important, but unmeasured aspects of plant functioning are not considered (Shipley et al. 2016). For this reason, phylogenetic data are often used as a proxy for the functional similarity of species in communities (Kraft et al. 2007). This phylogenetic approach is rooted in the simple idea that closely related species are ecologically/functionally more similar than more distant relatives (Burns & Strauss 2011). This relationship can be estimated using measures of phylogenetic signal on traits (Blomberg et al. 2003). In those cases where there is a strong signal, phylogenetic dispersion should reflect the functional dispersion since closely related species are expected to have similar trait values due to common ancestry (Cavender-Bares et al. 2004; Swenson et al. 2007; Swenson & Enquist 2009). However, when trait distribution has a low phylogenetic signal, phylogenetic data can provide information about unmeasured traits (Swenson & Enquist 2009; Peres-Neto & Kembel 2015).

Despite the large amount of work quantifying the functional and phylogenetic structure of communities over the past decade, a general picture regarding the processes driving assembly remains unclear. Although discrepancies between trait and phylogenetic dispersion are common (Swenson et al. 2007; Swenson & Enquist 2009), discrepant functional or phylogenetic patterns have also been found in communities due to differences in the spatial and temporal scales utilized (Swenson et al. 2006; Götzenberger et al. 2012). An explanation for seemingly conflicting results could be that different processes may be simultaneously operating at different scales,

in response to different environmental factors (Grime 2006; Vonlanthen et al. 2006), producing opposing effects (see Soliveres et al. 2012) sometimes difficult to predict.

Functional trait dispersion is frequently considered as an integrated response to single environmental gradients or to multiple, but independent gradients (de Bello et al. 2013; Schöb et al. 2013; Dainese et al. 2015). However, multiple gradients are rarely considered simultaneously (e.g. Swenson & Enquist 2007). To know how and to what extent communities respond to interacting gradients could explain discrepancies when functional and phylogenetic structures have been explored in modeled plant assemblages (May et al. 2013) or along a complete range of spatial scales (Chacón-Labella et al. 2016). For instance, hydraulic conductance and photosynthesis are governed by water availability, water potential gradients and temperature, which ultimately result from an interaction between precipitation and temperature and not from each factor independently (Thornthwaite 1948). Thus, it is important to evaluate the complementarity between functional and phylogenetic approaches by exploring whether or not they are redundant along complex and simultaneous environmental gradients and considering different spatial scales.

Here, we assessed plant functional trait and phylogenetic dispersion along interacting elevation and potential solar radiation gradients controlling the effect of the soil fertility and species spatial aggregation. This was done across multiple-spatial scales -plot (20 x 20m), subplot (2.4 x 2.4 m) and cell (30 x 30 cm)- to provide insights into the processes that drive community assembly. The study was performed in mountains of the Mediterranean-type climate zone of the central Chilean Andes. These habitats are an ideal model system to our objectives as they cover a wide elevational gradient where multiple abiotic variables exhibit gradients that are not co-

linear (Pescador et al. 2015). Our specific objectives were (1) to quantify phylogenetic and functional trait dispersion in communities along multiple abiotic gradients; (2) to determine the degree to which functional trait and phylogenetic dispersion are coupled across different spatial scales; and (3) to evaluate phylogenetic signal on functional traits to help to elucidate the degree to which phylogenetic information is providing novel information.

Methods

Study area

This study was conducted in three Andean massifs of the Mediterranean-type climate zone of central Chile (Appendix S1) nearly covering the complete latitudinal gradient where this ecosystem occurs in South America; more than 400 kilometers long: (1) Farellones 40 km east of the city of Santiago; (2) Morado at the Maipo River Basin, 80 km south-east of the city of Santiago; and (3) Maule, 100 km east of the city of Talca (see Table 1). The elevation in our study ranges from 2064 to 3627 m.a.s.l. The inter-annual rainfall variability is extremely high. Precipitation mainly occurs as snow during the winter. Summers are extremely dry and the summer drought increases at lower elevations.

Vegetation above the treeline in the Andes of Central Chile generally comprises prostrate shrubs (e.g. *Berberis empetrifolia* Lam.) and some annual species (e.g. *Chaetanthera euphrasioides* (DC.) F. Meigenat) at lower elevations, while at the higher elevation the community is dominated by cushion-like plants (e.g. *Azorella madreporica* Clos) and caespitose and rosette-forming perennial herbs (e.g. *Nassauvia pyramidalis* Meyen) (Cavieres et al. 2000).

Table 1. Geographic location, main climatic characteristics, treeline elevation and

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treeline species of the studied sites.

Study site	Location	Annual precipitation (mm)	Mean temperature (ºC)	Treeline elevation (m a.s.l.)	Treeline species
Farellones	33°20'S, 70°14'W	943[1]	6.5[2]	2200	*Kageneckia angustifolia* (Rosacea)
Morado	33°46'S, 70°01'W	1172[4]	8.7[3]	2100	*Kageneckia angustifolia* (Rosacea)
Maule	35°58'S, 70°30'W	900[5]	5[5]	1700	*Nothofagus antarctica* (Nothofagaceae) and *Austrocedrus chilensis* (Cupressaceae)

[1]Santibañez & Uribe (1990), [2]Cavieres, Peñaloza & Arroyo (2000),[3]Fabres (2009),

[4]Muñoz-Schiciu, Moreira-Muñoz & Villagrán (2000) and [5]Méndez (2014).

Experimental design

In the summer of 2014, we sampled 20 alpine sites above the treeline selecting representative patches of alpine vegetation (Appendix S1) avoiding screes, rocks and wet habitats. Vegetation was sampled at three different spatial scales (Appendix S1): 1) Plot scale: at each site, we established a 20 m x 20 m plot in a representative area with homogeneous vegetation and avoiding, rocks, screes, snow beds or humid depressions; 2) Subplot scale: five 2.4 m x 2.4 m subplots were established within each plot, one in each corner and a fifth in the center; 3) Cell scale: the central subplot was thoroughly divided into 64 cells of 30 cm x 30 cm. We registered the cover of

any plant species at each subplot and at each cell. Finally, the species cover at the plot scale was calculated as the average of the covers of each species in the five subplots.

We characterized the environment at each plot by determining several variables. Specifically, the elevation and aspect were obtained by using a GPS (Garmin Colorado-300, Garmin Ltd., Olathe, USA) and the slope using a clinometer (Silva Clinomaster, Silva Sweden, Sollentuna, Sweden). As the three zones are in different latitudes and this factor may influence community assembly, elevation was standardized by subtracting the treeline altitude from plot elevation. Local treeline limits were identified by Google Earth and averaging the elevation of conspicuous trees in the area. Aspect and slope values were used to calculate Gandullo's potential solar radiation coefficient (Gandullo 1974):

$$GIa = sen\, i \cdot \cos p \; - \cos \alpha \cdot \cos i \cdot sen\, p$$

$$GIb = sen\, i \cdot \cos p \; + \cos \alpha \cdot \cos i \cdot sen\, p$$

Where *GIa* is the potential solar radiation calculated in north-facing sites and *GIb* in south-facing sites, *i* is the solar incidence angle (i.e. 90º - latitude), *p* is the slope, *α* is the angle formed by the aspect and 0º for *GIa* and the aspect and 180º for *GIb*.

To assess soil fertility, two soil samples (5 cm in diameter and 10 cm deep) were collected at each corner-subplot; one in an open area and the other under a vegetated patch with the dominant species in the community. Soil samples were air dried for one month and sieved through a 2 mm mesh and eight parameters of functional ecosystem properties related to the cycling and storage of nutrients were estimated. Specifically, we estimated organic carbon (C), total nitrogen (N), available

phosphorus (P) and potassium (K) as key nutrients related to primary productivity and the buildup of nutrient pools (Maestre et al. 2012). In addition, we estimated Phosphatase and β-glucosidase soil enzymatic activities that are tightly related to soil microbial functionality and rapid nutrient dynamics. Further details regarding the estimation of soil properties are provided in Appendix S2. The two soil variables per subplot were used to obtain a subplot-level estimate of soil parameters. This was done by weighting the soil values using the mean cover observed for bare ground and vegetated areas in the subplot. The center subplot value was estimated as the average of four subplots at each site. With all of them we calculated the multifunctionality index proposed by Maestre et al. (2012) as an indicator of soil fertility.

Phylogenetic analysis

To estimate the phylogenetic diversity and relatedness, a molecular phylogeny was generated for the community using two barcoding loci (rbcL and matK). Phylogenetic analysis are explained in Appendix S3 and Primers for PCR, sequencing and PCR cycling conditions used in this study are provided in Appendix S4.

Plant functional traits

During the austral summer season of 2015 functional traits were measured for 71 species, which represented at least 80% of the cumulated cover of each subplot (Borgy et al. 2017). We measured six plant functional traits which *a priori* are expected to respond to the environmental conditions along the elevation gradient. Maximum plant height (MPH) represents a trade-off between competitive vigor (Cornelissen et al. 2003) and protection by snow cover (Körner 2003); plant size (SI) as a surrogate of accumulated resources (Pescador et al. 2015), leaf area (LA) is related to cold stress and drought (Cornelissen et al. 2003); specific leaf area (SLA) is

related to growth and photosynthetic capacity (Cornelissen et al. 2003); leaf dry matter content (LDMC) is related to investment in leaf tissues, storage and structural defense (Cornelissen et al. 2003); and leaf thickness (LT) that is related to nutrient cycling and resistance to wind (Choler 2005). All these traits were measured using standardized protocols (Cornelissen et al. 2003) with the exception of plant size (SI: Pescador et al. 2015), which was calculated as $SI = \pi \cdot L \cdot S/4$, where L is the longest diameter and S is the shorter diameter perpendicular to the former one.

Diversity estimates and statistical analyses

Functional and phylogenetic mean pairwise distances (MPD) weighted by cover values from each sampling unit (three scales) were compared to the patterns derived from a null model. We utilized an independent swap null modeling approach because species abundance was not correlated with traits and it was not phylogenetically structured (Blomberg's K < 0.001, P = 0.11 and Pagel's λ = 0.089, P = 0.54) (Blomberg et al. 2003; Hardy 2008). This null model randomizes the site-by-species community data matrix which maintains the observed species richness of communities (i.e. row sums) and the occupancy rates of species across the study system (i.e. column sums). We generated 999 random community matrices using the independent swap. The functional or phylogenetic dispersion we used to calculate the corresponding standardized effect size SES (SES: Gotelli & McCabe 2002) where positive values indicated more observed diversity than expected (i.e. overdispersion) and negative values indicated less diversity than expected (i.e. clustering). It is worth noting that the dispersion values were considered emergent properties of the realized assemblage at each spatial scale independently of the fact they were significant or not

in relation to a specific null model. Before analysis, the traits were log-transformed to reach normality when necessary and centered by their standard deviation.

We tested whether functional and phylogenetic diversity provided similar patterns due to phylogenetic signal (i.e. tendency for closely related species to be more similar) assessed with the K statistic of Blomberg and with Pagel's λ using a Brownian motion model of trait evolution (Pagel 1999; Blomberg et al. 2003).

The effects of two coincident abiotic gradients, elevation, potential solar radiation and their interaction, on the functional and phylogenetic dispersion were analyzed using linear models at the plot scale and generalized linear mixed models (GLMM) at subplot and cell scales. Zone (massif) and plot were considered a fixed effect and a random effect respectively to take in account the longitudinal dependences of the data.

In addition, we considered two other fixed predictors, soil fertility and the biotic interactions measured as the checkerboard score (C-score: Stone & Roberts 1990) in order to have a statistical control of these sources of community variation. The C-score calculated with the cell data, gives an estimate of the degree of spatial segregation in species occurrences, a useful indicator of plant-plant interactions and niche differentiation at the community level (Gotelli 2000).

Before assessing the models, multi-collinearity was checked using a generalized variance inflation factors (Fox 2015). In all cases they were below 2, suggesting the absence of collinearity (Chatterjee & Hadi 2001). We select the best model based upon Akaike's information criterion corrected for small samples (AICc). Models with a difference in AICc (ΔAICc) <2 were considered to be indistinguishable (Burnham & Anderson 2002) and an average explicatory model was estimated. We

calculated Akaike weights (wi) to evaluate the importance of each predictor (Burnham & Anderson 2002), and it relative importance (w+) was assessed by summing of wi values of each candidate model in which the predictor appeared.

Functional and phylogenetic analyses were conducted with the R package *Picante*, the linear models and the linear mixed models with R package *lme4* and

Dispersion/ Predictor variable	plot	subplot	cell

model selection and calculation of the coefficient of determination with package *MuMIn.*

Results

We sampled 100 subplots, distributed in 45 (Maule), 25 (Morado) and 30 (Farellones) subplots. We register 70, 43 and 50 species in the three massifs, respectively, and 105 species in total (see Appendix S5 for a list of all species). The number of species per plot ranged from 12 to 33 with a mean value of 20.8; for subplot those figures ranged from 3 to 22 with a mean value of 11.2; and for cell, they ranged from 3 to 22 with a mean value of 5.5. The most abundant species in the Maule were graminoids as *Festuca acanthophylla* E. Desv. and *Poa denudata* Steud. In the other two massifs, graminoids *Rytidosperma pictum* (Nees & Meyen) Nicora and *Poa denudata* together with cushion-like shrubs such as *Azorella madreporica* Clos and *Laretia acualis* (Cav.) Gillies & Hook. dominated the alpine vegetation.

Table 2. Model-averaged estimates of model selection and multimodel inference for functional and phylogenetic dispersions.
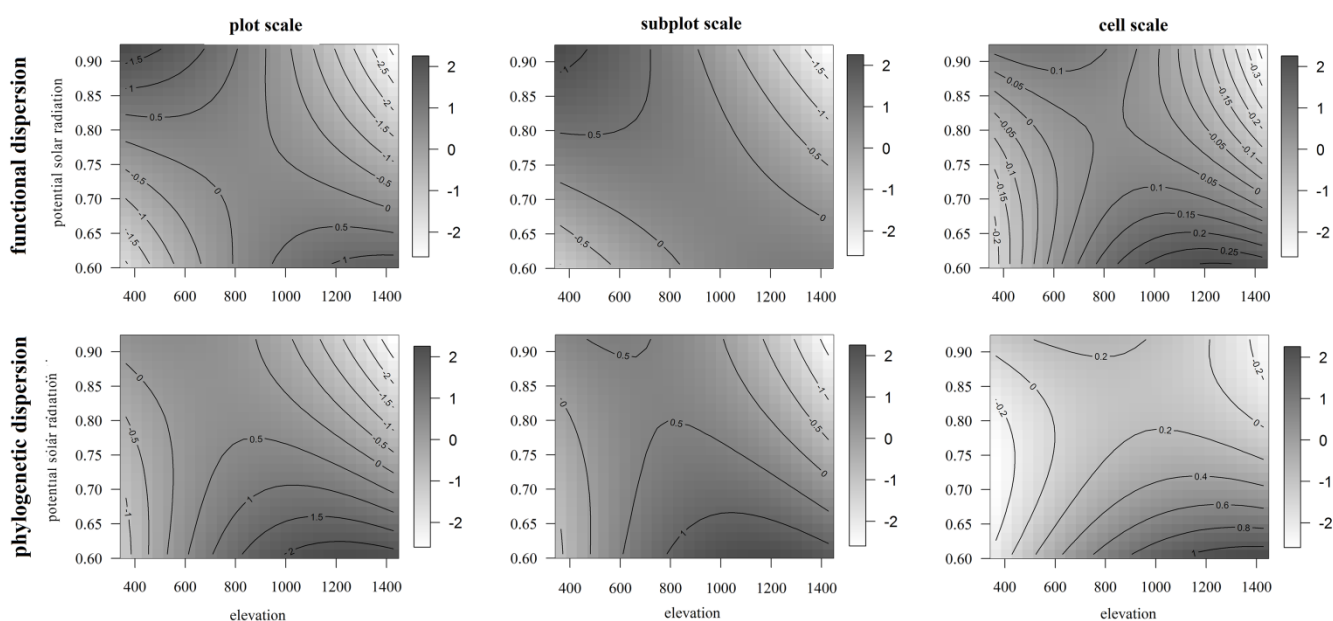
Functional dispersion			
elevation	0.020	0.011	0.003
potential solar radiation	23.280	10.687	2.714
elevation X potential solar radiation	-0.027	-0.014	-0.003
c-score	-	-0.010	-
soil fertility	-	-	0.005
Phylogenetic dispersion			
elevation	0.020	0.012	0.005
potential solar radiation	13.93	8.306	3.396
elevation X potential solar radiation	-0.022	-0.014	-0.005
c-score	-	-0.004	-0.002
soil fertility	-	-	0.005

Functional dispersion

The functional MPDs were highly variable among communities and relatively constant across scales, averaging 2.02 per plot (range = 0.47 - 3.21), 2.11 per subplot range = 0.10 - 3.60), and 1.43 per cell (range = 0.01 - 3.68). Functional dispersion in the community was significantly influenced by the abiotic factors at any spatial scale (Table 2). In general, the predictor variables with the highest relative importance ($w+$) were elevation, potential solar radiation and their interaction (Appendix S6). In particular, the increase in elevation produced a shift from relatively low dispersion values suggesting trait clustering to larger values suggesting overdispersion (Fig. 1). There was also a general increment in overdispersion with increasing potential solar radiation (Fig. 1). Furthermore, the interaction between these two variables produced clustering when there was a simultaneous increase in elevation and potential solar radiation (Fig. 1). The effect of these two variables was consistent across the different spatial scales (Table 2). At subplot scale, functional trait overdispersion also occurred when aggregated spatial patterns of species predominated (i.e. higher C-score values)

suggesting an aggregation of functionally dissimilar species, and clustering when species tend to segregate (Appendix S7).

Figure 1. Predicted relationship of the functional (left) and phylogenetic dispersion (right) with the interaction of potential solar radiation and elevation across plot, subplot and cell scales (from top to bottom). The tone scale on the right of each map indicates the dispersion values. Values > 0 indicate overdispersion. Values < 0

indicate clustering. The black lines represent isoclines.

A significant relationship between the soil fertility index and the functional dispersion was also found (Table 2) but at the finest scale. An overdispersed pattern in higher fertility levels (i.e. more fertile soil) and a clustered pattern in lower levels of fertility at cell scale was observed (Appendix S7).

Phylogenetic dispersion

The average phylogenetic MPDs were 0.23 per plot (range = 0.06 - 0.32), 0.22 per subplot (range = 0.12 – 0.35), and 0.15 per cell (range = 0.0003 – 0.34). We found similar relationships between the abiotic gradients and phylogenetic dispersion to

those of the functional dispersion analyses. In particular, the interaction between elevation and potential solar radiation explained most of the variability of the models at the three spatial scales considered (Table 2; Fig. 1). Regarding soil fertility and C-score index effects, we observed the same trends that were observed for functional dispersion.

Phylogenetic signal of functional traits

The Blomberg's K statistic was lower than 0.002 for all the functional trait measured, indicating phylogenetic signals lower than that expected from a Brownian motion model of trait evolution. However, Pagel's λ indicated rather low phylogenetic signals in all traits except for leaf area where no signal was found (LA: $\lambda=0.69$, $P>0.05$).(SI: $\lambda=0.84$, $P<0.001$; MPH: $\lambda=0.24$, $P<0.01$; SLA: $\lambda=0.56$, $P<0.05$; LDMC: $\lambda=0.66$, $P<0.001$; LT: $\lambda=0.59$, $P<0.05$). The low phylogenetic signals found corresponded to the Spearman correlation between phylogenetic and functional trait dispersion matrices (0.69, 0.65 and 0.67 (P-values < 0,001) at plot, subplot and cell scales respectively).

Discussion

Functional and phylogenetic dispersion along interacting abiotic gradients at different spatial scales provides valuable information about the processes underlying community structure and assembly (Kawai & Tokeshi 2007). Moreover, our results reinforce the notion that in order to unveil assembly mechanisms not only different spatial scales need to be considered (Messier et al. 2010; Spasojevic & Suding 2012), but also interacting environmental gradients.

While much effort has been devoted to quantifying the functional similarity of species in communities without reference to the abiotic environment (Kraft et al. 2008; Swenson et al. 2012), the tradition in trait-based ecology of relating functional trait means to environmental gradients has naturally lead to the study of functional dispersion along these same gradients (Schöb et al. 2013; Dainese et al. 2015). Although studies focused on one main gradient such as elevation (Read et al. 2014; Pescador et al. 2015), potential solar radiation (Ackerly et al. 2002) or soil nutrient availability (Yang et al. 2014) are useful because they allow a closer investigation into the abiotic mechanisms shaping community diversity and assembly, studies evaluating several gradients at the same time (de Bello et al. 2013; Liu et al. 2013; Xu et al. 2017), including their interaction, are particularly important because communities may be structured in relation to the total environment they experience and not just to a single gradient.

Functional dispersion (i.e. SES of the mean pairwise distance) was influenced by potential solar radiation, a surrogate of energy input that strongly affect important processes (e.g. snowmelt, soil water content, etc.) with critical consequences for plant performance including phenology, plant water content and photosynthesis (Holland & Steyn 1975; Cornwell & Ackerly 2009). This effect differed along elevation as noted by the significant interaction between these two factors (Fig. 1). Functional trait dispersion showed relatively high values suggesting overdispersion in two different environmental scenarios: first when high elevations coincide with low potential solar radiation (i.e. a cold environment) and second, at low elevations but with high potential solar radiation (a rather hot and dry environment) (Fig. 1). These abiotic combinations results in probably the most stressful conditions that can be found in our study sites (see Ackerly et al. 2002; Cavieres et al. 2007; Giménez-Benavides et al.

2007). It is well known that temperature decreases with elevation with freezing temperatures affecting the diversity in higher elevations (Körner 2007). Moreover, in Mediterranean mountains, the short period of vegetative activity is conditioned simultaneously by the strong summer drought typical of this climate shortening the vegetative growth period. This occurs in opposition to the cold stress gradient of mountains, exacerbating harsh conditions at low elevations (Giménez-Benavides et al. 2007; Körner 2007; Mihoč et al. 2016). Therefore, high potential solar radiation would aggravate drought stress in the lower elevations areas, while low potential solar radiation add environmental harshness to the low temperatures at higher elevations.

The current paradigm suggests that stressful conditions should induce clustered functional diversity patterns due to filtering processes (Cavender-Bares et al. 2006; de Bello et al. 2009), but this is not the case in our Mediterranean climate-type mountains. This could be caused by the incidence of biotic interactions (Pausas & Verdú 2010). Many studies have shown the high importance of biotic interactions as drivers of community assembly (Butterfield & Callaway 2013), also in alpine systems (Mitchell et al. 2009; Schöb et al. 2013; Anthelme et al. 2014). Both positive (i.e. facilitation) and negative (i.e. competition) interactions can generate overdispersion patterns (Soliveres et al. 2012; Gross et al. 2013; Pistón et al. 2015). Overall, facilitation tends to dominate interactions when environmental harshness increases (Callaway et al. 2002; Butterfield & Callaway 2013), whereas when conditions tend to be milder, competition generally increases its importance (MacArthur & Levins 1967; Michalet et al. 2006). Although in alpine habitats a gradient from facilitation dominance in high elevations to competition in the more benign low elevations seems to be the norm (Callaway et al. 2002) a humped-back pattern with maximum stress at the two edges of the gradient (i.e. coldness at the top and summer drought at the low)

seems to be typical in Mediterranean mountains (Giménez-Benavides et al. 2007; Pescador et al. 2015) including the Mediterranean Andes (Cavieres et al. 2006). Interestingly, species spatial aggregation (lower C-scores) was related with functional and phylogenetic overdispersion, while species segregation (higher C-scores) generated functional clustering (Table 2). This result suggests the prevalence of facilitation in the local assembly (Götzenberger et al. 2012) because nurses and facilitated plants having divergent trait values are phylogenetically distant, as it has been also shown in other studies including alpines sites (Butterfield et al. 2013; Pistón et al. 2015)., Thus, the low functional diversity and convergence where environmental conditions are milder suggest that competition may be the underlying process responsible for this pattern. Although plant-trait based and community assembly literatures have usually suggested that competition drives functional and/or phylogenetic overdispersion (Cavender-Bares et al. 2004), functional and phylogenetic convergence may also be the result of processes such as competitive dominance of some few more competitive species (Mayfield & Levine 2010; HilleRisLambers et al. 2012; Kunstler et al. 2012).

Our findings also suggest that soil fertility may be particularly important in determining the functional structure but only at the finest spatial scale. Soil fertility operated as an abiotic determinant increasing functional clustering when soil fertility was lower (limitation of primary productivity). By contrast, when soil fertility was high, an overdispersion pattern emerged (Table 2). These findings suggest community assembly is mediated by limiting similarity that repulses functionally similar species (MacArthur & Levins 1967), therefore, niche differentiation is required to avoid competition exclusion (Aarssen 1983). Similar results have previously been found in other plant communities when functional diversity is related with different ecosystem

functions. For example, Laliberté *et al.* (2013) found increased functional diversity with higher levels of productivity and decreased with low levels in semi-arid grasslands and Mason *et al.* (2012) found divergence and convergence at high and low fertility respectively in rain forest communities.

When the results of phylogenetic dispersion were evaluated, the patterns of the effect between potential solar radiation and elevation, together with the effect the C-score index and the soil fertility were similar to those of the functional dispersion, and consistently at all scales (Table 2). The analysis of phylogenetic signal using Blomberg's K statistic revealed no signal for the plant functional traits studied whereas Pagel's λ indicated a phylogenetic signal present in all traits (except for leaf area), but of low intensity. Under the current theoretical framework if both functional and phylogenetic dispersions are similar, functional trait patterns would show a strong phylogenetic signal (Kraft et al. 2007; Cadotte et al. 2013; Gerhold et al. 2015; de Bello et al. 2017). However, this does not need to be the case because unmeasured traits with stronger phylogenetic signal that are low correlated with traits of interest may similarly respond to the gradients. This finding reinforces the idea that the phylogenetic information is complementary to the functional information (Swenson & Enquist 2009) rather than being redundant information or a proxy of the functional structure (Mason & Pavoine 2013; Pavoine et al. 2013). Our results also suggest that the strength of local assembly processes remains strongly connected with spatial scales (Chalmandrier et al. 2017). Thus, functional trait and phylogenetic dispersion were coupled consistently across spatial scales. Many studies have showed that discrepancies with different patterns of dispersion, functional or phylogenetic, occur among different spatial scales (Cavender-Bares et al. 2006; Swenson et al. 2007; Yang et al. 2014). In our case, probably due to the sharp shifts in environmental

abiotic conditions along a long elevational gradient, the dispersion patterns remain similar and tight across scales.

Taken together our results suggest the dominance of abiotic gradients interactions in the functional and phylogenetic dispersion structure although they also reinforce the general idea that biotic interactions and other very fine local factors such as soil fertility heterogeneity are simultaneously operating.

Conclusions

Our results indicate the importance of evaluating more than one abiotic gradient at a time. Interactions (additive or synergistic) between gradients are expected to be common and analyzing these interactions can give novel perspectives to the community assembly processes. Our study demonstrates how these interactions may act. Stress in these mountains is very intense at both ends of the elevational gradient due to the existence of opposite temperature and moisture stress gradients (Mihoč et al. 2016). Solar radiation must be taken into account since it can attenuate or exacerbate environmental harshness associated to elevation. This interaction between both factors produced functional and phylogenetic overdispersed patterns resulting from facilitative interactions where the conditions are more stressful. On the contrary, where the conditions are milder, dominance of a few species that are more competitive could lead to clustered patterns. Thus, our results support the hypothesis that biotic interactions modulated by environmental conditions are important for alpine plant community assembly. These patterns were consistent across spatial scales. Finally, it is worth to note that the functional and phylogenetic patterns and drivers run in parallel despite the fact that the considered functional traits had no phylogenetic signal. This suggest that first, the two diversities are not redundant

(Swenson & Enquist 2009), and second, the extreme abiotic conditions these communities face produce convergence in the patterns and mechanisms of these two complementary diversities.

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Supporting information to the paper

López-Angulo et al. Interactions between abiotic gradients determine functional and phylogenetic diversity patterns in Mediterranean-type climate mountains in the Andes. *Journal of Vegetation Science.*

Appendix S1. Schematic of experimental design. **a)** Localization of study areas in the central Chilean Andes; **b)** plot distribution in each zone; **c)** typical structure of vegetation; and **d)** sampling design structured across three scales.
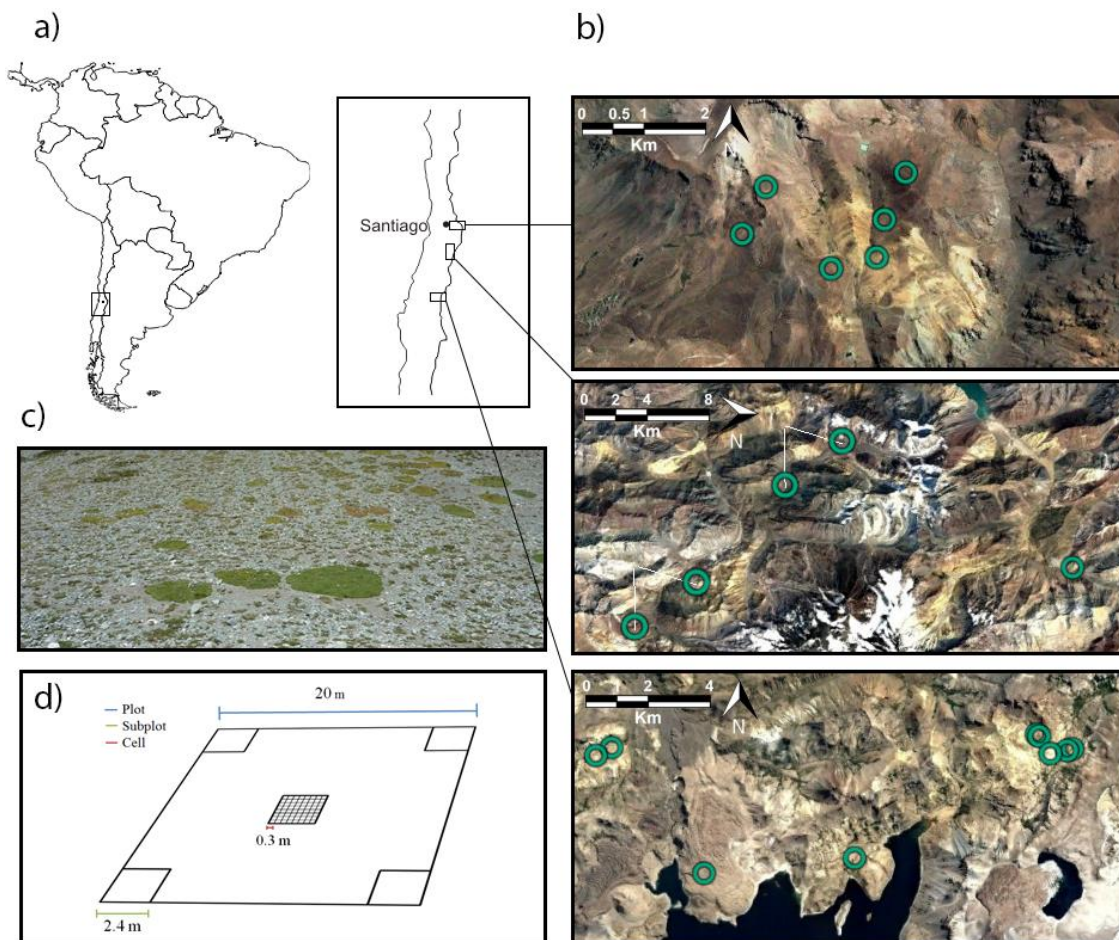
Appendix S2. Methods of estimation of soil properties.

Soil organic C was determined by colorimetry after oxidation with a mixture of potassium dichromate and sulphuric acid (Yeomans & Bremner 1988). Total N and available P was determined on a SKALAR++ San Analyzer (Skalar, Breda, The Netherlands) in the Nutrilab/URJC lab after digestion with sulphuric acid and Kjedahl´s catalyst (Anderson & Ingram 1994). Potassium (K) was measured with the same analyzer after the soil samples had been shaken with distilled water (1:5 ratio) for 1 h. Ezimatic activities were estimated using the methodology described in Eivazi & Tabatabai (1988; β-glucosidase) and Tabatabai and Bremner (1969; acid phosphatase).

Anderson, J.M., & Ingram, J.S.I. 1994. Tropical soil biology and fertility: A handbook of methods. Soil Science 157: 265.

Eivazi, F., & Tabatabai, M.A. 1988. Glucosidases and galactosidases in soils. Soil Biology and Biochemistry 20: 601–606.

Tabatabai, M.A., & Bremner, J.M. 1969. Use of p-nitrophenyl phosphate for assay of soil phosphatase activity. Soil biology and biochemistry 1: 301–307.

Yeomans, J.C., & Bremner, J.M. 1988. A rapid and precise method for routine determination of organic carbon in soil. Communications in Soil Science and Plant Analysis 19: 1467–1476.

Appendix S3. Phylogenetic analysis

In the first instance, available species sequences from GenBank were downloaded (45 sequences). The rest of the species sequences (165 sequences) were obtained in the laboratory. Specifically, 20 mg of fresh leafs was collected from three individuals per species. The samples were then disrupted and homogenized with a TissueLyser LT (Qiagen, Valencia, CA, USA) using glass beads after storing and drying in silica-gel for one month. Total DNA was extracted with DNeasy Plant Mini-Kit (Qiagen, Valencia, CA, USA) following the manufacturer's instructions.

The rbcL barcode was amplified in a 25 µL reaction with 2 µL of DNA in 23 µL mix-reaction -2.5 µL of Ta buffer 2 mM with MgCl2, 1 µL of dNTP Mix (0.4 mM), 1.25 µL of reverse and forward primer and 1.25 U Taq DNA Polymerase (Biotools, Madrid, Spain)-. The matK barcode was amplified by puReTaq Ready-To-Go PCR beads (Amersham Pharmacia Biotech, Uppsala, Sweden). PCR amplification was performed on a S1000 Thermal Cycler (Bio-Rad, Hercules, CA, USA). Primers for PCR, sequencing and PCR cycling conditions used in this study are provided in Appendix S4. Other primer pairs were necessary for samples that either failed in PCR amplification (see Appendix S4). Amplified PCR products were purified using the ExoSap purification kit® (USB Corporation, Cleveland, OH, USA). The samples were sequenced by MACROGEN (Seoul, Korea and Amsterdam, Netherlands). In order to corroborate the species identity two individuals were used to obtain the forward and reverse strands. Consensus sequences were assembled using Sequencher 4.1.4 software (Gene Codes Corporation, Ann Arbor, MI, USA) and aligned with MAFFT online v. 7, then checked manually with Mesquite version 2.6. Phylogenetic analyses were conducted with the R package *phangorn* (Schliep 2011) using the maximum likelihood model with 100 bootstrap replications. To obtain phylogenetic tree we used a species pool composed by the species of this study together with similar ecosystem species from South of Chile and Spain. In total, we used 573 DNA sequences of which 105 appeared in our sample area.

Schliep, K.P. 2011. Phangorn: phylogenetic analysis in R. Bioinformatics 27: 592–593.

Appendix S4. Primers, sequences and PCR conditions used in this study for barcoding loci rbcL and MatK.

Barcoding locus	Primer	Direction	Sequence (5′ → 3′)	PCR conditions	Ref.
rbcL	rbcl-F	F	ATGTCACCACAAACAGAGACTAAAGC	95ºC 3min; [34 cycles: 94ºC 30s; 52ºC 40s ; 72ºC 1min]; 72ºC 10min	1
	rbcl-R	R	GTAAAATCAAGTCCACCRCG	95ºC 3min; [34 cycles: 94ºC 30s; 52ºC 40s ; 72ºC 1min]; 72ºC 10min	1
	1F	F	ATGTCACCACAAACAGAAAC	95ºC 3min; [34 cycles: 94ºC 30s; 52ºC 40s ; 72ºC 1min]; 72ºC 10min	2
	724R	R	TCGCATGTACCTGCAGTAGC	95ºC 3min; [34 cycles: 94ºC 30s; 52ºC 40s ; 72ºC 1min]; 72ºC 10min	2
Matk	KIM 1R	F	ACCCAGTCCATCTGGAAATCTTGGTTC	95ºC 3min; [36 cycles: 94ºC 30s; 58ºC 40s ; 72ºC 1min]; 72ºC 10min	3
	KIM 3F	R	CGTACAGTACTTTTGTGTTTACGAG	95ºC 3min; [36 cycles: 94ºC 30s; 58ºC 40s ; 72ºC 1min]; 72ºC 10min	3
	xF1	F	TAATTTACGATCAATTCATTC	95ºC 3min; [36 cycles: 94ºC 30s; 58ºC 40s ; 72ºC 1min]; 72ºC 10min	4
	MALPR12	R	ACAAGAAAGTCGAAGTAT	95ºC 3min; [36 cycles: 94ºC 30s; 58ºC 40s ; 72ºC 1min]; 72ºC 10min	4
	390F	F	CGATCTATTCATTCAATATTTC	95ºC 3min; [34 cycles: 95ºC 1min; 48ºC 40s ; 72ºC 1min]; 72ºC 10min	5
	1326R	R	TCTAGCACACGAAAGTCGAAGT	95ºC 3min; [34 cycles: 95ºC 1min; 48ºC 40s ; 72ºC 1min]; 72ºC 10min	5

1. Kress, W.J., Wurdack, K.J., Zimmer, E.A., Weigt, L.A. & Janzen, D.H. 2005. Use of DNA barcodes to identify flowering plants. *Proceedings of the National Academy of Sciences*, **102**, 8369–8374.

2. Fay, M.F., Swensen, S.M. & Chase, M.W. 1997. Taxonomic affinities of *Medusagyne oppositifolia* (Medusagynaceae). *Kew Bulletin*, 111–120.

3. Ki-Joong Kim, School of Life Sciences and Biotechnology, Korea University, Seoul, Korea, unpublished primers.

4. Dunning, L.T. & Savolainen, V. 2010. Broad-scale amplification of matK for DNA barcoding plants, a technical note. *Botanical Journal of the Linnean* Society, **164**, 1–9.

5. Cuénoud, P., Savolainen, V., Chatrou, L.W., Powell, M., Grayer, R.J. & Chase, M.W. 2002. Molecular phylogenetics of Caryophyllales based on nuclear 18S rDNA and plastid rbcL, atpB, and matK DNA sequences. *American Journal of Botany*, **89**, 132–144.

ppendix S6. Results of model selection and multimodel inference for functional and phylogenetic dispersion at three studied scales. We detailed the ΔAICc < 2 set of models. X indicates variable inclusion in each individual model. wi: Akaike weights. w+: relative importance of each predictor for each averaged model.

Dispersion/Scale/ Models		elevation	potential solar radiation	elevation X potential solar radiation	C-score	Fertility	AICc	ΔAIC$_c$	wi
Functional dispersion									
plot									
1		X	X	X			63.8	0	1
	w+	1	1	1	-	-			
subplot									
1		X	X	X	X		244.5	0	0.703
2		X	X	X			245.6	1.13	0.297
	w+	1	1	1	0.63	-			
cell									
1		X	X	X		x	1432.9	0	0.53
2							1434.2	1.21	0.257
3		X	X	X			1434.5	1.58	0.213
	w+	0.78	0.78	0.78	-	0.40			
Phylogenetic dispersion									
plot									
1		X	X	X			60	0	1
	w+	1	1	1	-	-			

subplot

1	X	X	X			220.9	0	0.543
2	X	X	X	X		221.0	0.04	0.457
w+	1	1	1	0.49	-			

cell

1	X	X	X			1463.0	0	0.4
2	X	X	X	X		1463.8	0.79	0.273
3	X	X	X		X	1464.7	1.69	0.167
4	X	X	X	X	X	1464.8	1.75	0.159
w+	1	1	1	0.43	0.33			

Appendix S7: Relationships between the functional dispersion (left) and phylogenetic dispersion (right), with C-score index (a, b and e) and soil fertility (c and d) for the GLMM models. The fitted lines indicate results from GLMMS with confidence intervals.

subplot scale
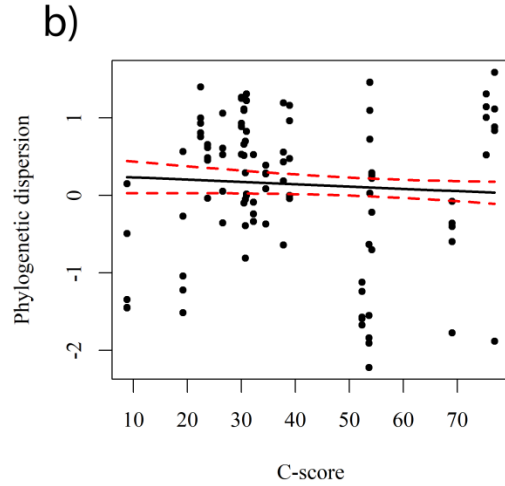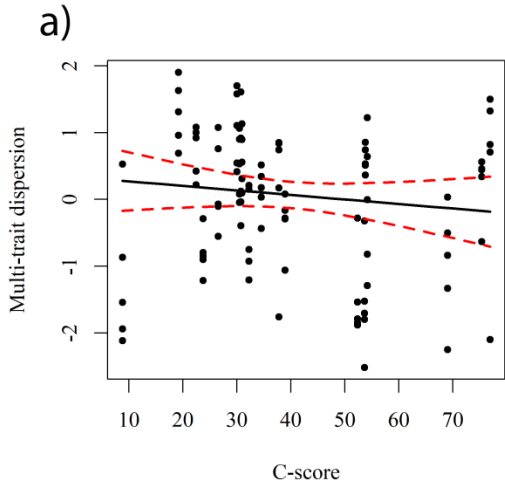
cell scale
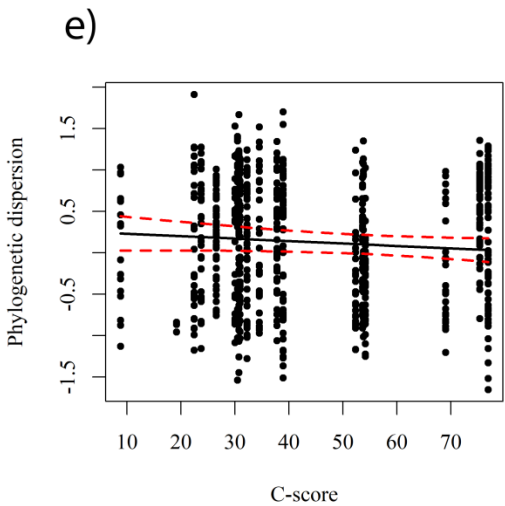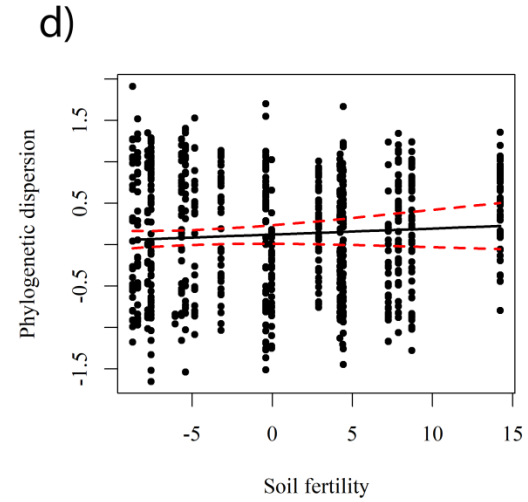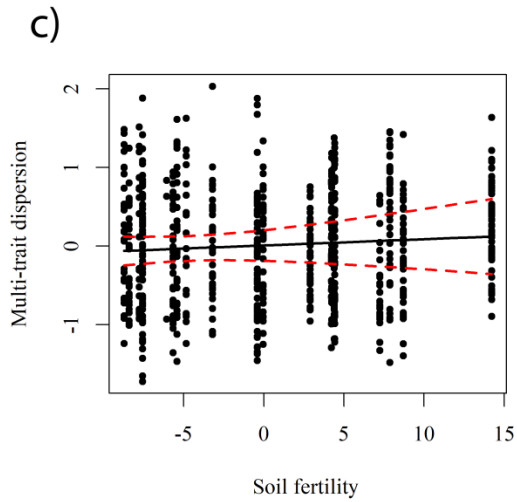
Capítulo 3

Biotic interactions at the edges of abiotic gradients shape

functional structure in an alpine plant community: a novel

null model approach

Jesús López-Angulo, Marcelino de la Cruz y Adrián Escudero

Abstract

A persistent challenge in Community Ecology is to understand plant community assembly and the underlying deterministic mechanisms of species co-existence. One of the most extensively used approaches to disentangle the role of these deterministic mechanisms in specific communities have been the so-called null modeling approach. However, despite of the potential of this approach, they have a reduced capacity to separate specific ecological processes.

Here, we propose the systematic use of three types of null models, each one able to reproduce the assembly of plant communities under the action of different assembly ecological rules (biotic, abiotic and a mix of both rules). Besides, we evaluate the discrepancies between observed and expected patterns under the three null models along three abiotic gradients (elevation, solar radiation and soil fertility) to shed light on the prevalence of each ecological rule along such gradients. With this in mind, we surveyed the alpine vegetation along a large elevational gradient in the central Pyrenees.

Although the three models were able to reproduce realistically the observed functional structures with a notable reduced number of significant deviations, we found significant discrepancies between observed and expected FD values along environmental gradients. We found positive effects of elevation on the discrepancies between observed and expected functional diversity estimated as the SES values (termed FD henceforth) in maximum plant height, leaf thickness and multi-trait combo identified in the case of the abiotic null model, as well as the negative relationship between potential solar radiation with FD of seed mass and maximum plant height. In the case of the biotic null model, we found only a positive significant effect of elevation over the FD of maximum plant height.

The patterns of functional convergence in plant height and seed mass support the idea that in more relatively benign conditions trait convergence patterns can be due to competitive processes, which sort species with different competitive abilities. Whereas, the greater functional diversity in maximum plant height, leaf thickness and in multi-trait variability produced with increasing altitude support the 'stress-gradient hypothesis' which suggest that facilitation become more important than competition as environmental stresses increases. Generating null assemblages under the action of a particular ecological assembly rule allow to compare observed and expected patterns and to decide if findings in the natural communities are compatible with such an ecological rule. Specifically, our results highlighted the potential of the environmentally constrained null to test for the effect of biotic interactions such as facilitation or competition.

Introduction

Understanding plant community assembly and the underlying mechanisms of species co-existence is a persistent challenge in Community Ecology (Weiher & Keddy 1995; Lortie et al. 2004; HilleRisLambers et al. 2012). Plant species composition of a natural assemblage is the net result of stochastic and deterministic processes acting simultaneously (Vellend et al. 2014; Escudero & Valladares 2016). A consensus exists that among the deterministic processes, sometimes called ecological assembly rules, the limitations imposed by the abiotic environment together with plant-plant interactions are critical (Götzenberger et al. 2012). Unfortunately, disentangling the effects of both types of processes, abiotic and biotic, under field conditions remains complicated. Trait-based ecology (see Shipley et al. 2016) provides a complete toolbox to solve such dilemma. The idea that all the species are ecologically equivalent is not easily defensible (Doncaster 2009), so a natural step forward is to consider their individual roles in the community based on each species' plant life-history and ecological traits (Keddy 1992; Diaz et al. 1998). Under this functional perspective the species thriving together in a realized assemblage have been first selected from the regional species pool by abiotic filters acting at relatively coarse spatial scales according to their plant functional traits (Lavorel & Garnier 2002; Mayfield et al. 2009). Secondly, they have outcompeted other species that passed the first filter but whose functional traits provided them with inferior competitive abilities (MacArthur & Levins 1967; Chesson 2000).

To date, one of the most extensively used approaches to disentangle the role of these deterministic mechanisms in specific communities have been the so-called null modeling approach (see Gotelli & Graves 1996). This powerful approach is based on the comparison of the distribution of values for any functional feature observed in

natural assemblages with those expected from randomly assembled communities. Unfortunately, despite the many null model algorithms (e.g., Hardy 2008; Botta-Dukát & Czúcz 2016; Götzenberger et al. 2016; Miller et al. 2017; Perronne et al. 2017) and randomization schemes (Cornwell et al. 2006; de Bello et al. 2012; Chalmandrier et al. 2013; Miller et al. 2017) available in the literature, there is a lack of general consensus on which are the most appropriate algorithm and randomization schemes to respond specific ecological questions (Ulrich & Gotelli 2013; Ulrich et al. 2017). Most null models used to assess the functional structure of the community are based on the randomization of species occurrences according to one or several well known matrix rules (Gotelli & Graves 1996), e.g., maintaining each species frequency (in order to account for ecological differences among species) and/or restricting sample species (in order to control for differences in soil fertility or other microsite conditions among sites) (Gotelli 2000; Gotelli & Entsminger 2003). However they have a reduced capacity to separate specific ecological processes (Gotelli & Ulrich 2012). Hence, a good choice among these null models is critical since can lead to very different conclusions (de Bello 2012).

In order to minimize the limitations of traditional null models based on reshuffling species, we need more realistic approaches able to reproduce assemblages under explicit assembly processes. In this case, if the observed pattern is not significantly different from expectations, we could not rule out such a process as an ecological deterministic rule. Deviations from these null expectations would reflect the implication of other not considered mechanisms (Gotelli & Ulrich 2012). For instance, the simplest way to generate environmentally constrained null communities is randomizing species composition within sites sharing a common habitat, elevational stratum or vegetation belt (Hausdorf & Hennig 2007; Jung et al. 2010; de Bello 2012).

Among other problems, this simple approach suffers, however, from the inherent loss of information associated to discretizing environmental gradients, including equalizing niche breath for groups of species. To solve some of these issues, some authors (e.g., Cornwell & Ackerly 2009; de Bello et al. 2012) have considered species-centred null models of niche breath based on the range (i.e., the extremes) of values measured for the relevant environmental variable(s) among the sites where each species has been observed. These models, however, assign the same probability of occurrence in a plot to all species whose niche breath includes the environmental conditions of the plot, irrespectively of whether those conditions are on the verge of species' niche breath or close to its ecological optima. Taking one step further, Peres-Neto et al. (2001) proposed estimating the probabilities of species occurrence as a function of environmental conditions using classification techniques such as linear discriminant analysis or logistic regression. Null models based on this approach could be employed to assemble null communities where species presence would fit the site's abiotic conditions. Nevertheless, patterns of functional convergence revealed on the basis of any of these "*classical*" null models have been generally attributed to environmental forces without taking into consideration that in fact they are the response to both biotic and abiotic mechanisms (Kraft et al. 2015; Cadotte & Tucker 2017). Incorporating some kind of biotic constraints in null models of community assembly could aid disentangling and/or evaluating the relative importance of biotic vs abiotic processes in the filtering of funtional attributes of the community. However, we do not know of any attempts to incorporate biotic constrains into null models of community assembly (but see D'Amen et al. 2017), even when there is an ample consensus that considering biotic interactions improves the ability of statistical models to predict species occurrences (Godsoe & Harmon 2012; Kissling et al. 2012; Anderson 2017). For example, it has been stated

that the so-called "community based modeling of species distributions" (Ferrier & Guisan 2006) is able to capture meaningful biotic interactions among species, improving the prediction of individual species occurrences(Baselga & Araújo 2009).

In this paper, we propose the systematic use of three types of null models, each one able to reproduce the assembly of plant communities under the action of specific ecological rules. More specifically, we generate null assemblages responding only to abiotic determinants, to biotic interactions, and to both, biotic and abiotic ecological rules. The comparison between the functional structures of the observed assemblages a those of the assemblages generated by these three kinds of null communities will help to unveil what assembly rules are involved and could give information on the prevalence and deviations of specific assembly processes in the field along environmental gradients.

For the abiotic null model based on abiotic we fitted binomial generalized linear models based on environmental predictors measured in the field (including climatic and soil covariates) to the presence/absence of each. By doing this, each species entered in the null communities as a probabilistic function of the abiotic conditions found in each site (*i.e.* niche preferences). These null models would be generating null communities responding exclusively to the abiotic conditions of each site. For the biotic null models, we fitted species' occurrence probabilities using Beals smoothing (Beals 1984; De Cáceres & Legendre 2008) which estimates the probability of encountering a given species at a site as a function of the pattern of species co-occurrences in the observed community. Therefore, this model would assemble null communities based mostly on the realization of species (i.e., biotic) interactions. In the third kind of null model, i.e., based on the biotic plus abiotic constraints, probabilities of occurrence for each species

were estimated following the recently proposed joint species distribution model framework (Pollock et al. 2014; Warton et al. 2015) where binomial GLM's of each species presence and absence are fitted to both environmental covariates and latent variables describing correlation between species (Hui 2016). Thereby, the null communities are generated with the estimated likelihood of species occupancy at each site including both its response to the abiotic environment and biotic interactions. In summary, we would have null communities after taken into consideration, only the abiotic limitations, the biotic interactions or both. A thorough comparison between the functional structure of the observed and null communities could give solid insights of which assembly rules these communities obey. Even more, the evaluation of the discrepancies between the expected and observed functional structures for each ecological rule along some abiotic gradient could shed light on the prevalence of each rule along such gradient.

With this in mind, we have surveyed the alpine vegetation along a large elevational gradient from 1660 to 2530 m in central Pyrenees. The vegetation presents a marked zonation and high turnover rate that suggest the prevalence of deterministic processes in the organization of the realized assemblages (Ninot et al. 2007), allowing us to explore the response of the functional structure of the communities to such assembly rules. We examined the prevalence of the assembly processes from responses of functional diversity to three critical key environmental factors -elevation, soil fertility and potential solar radiation-. We addressed the following specific questions: (i): (1) Could the use of environmentally and/or biotically constrained null models combined with functional trait distribution allow inferring assembly rules? (2) Which kind of mechanisms (biotic or abiotic) are responsible for the observed functional structure of the communities?

Methods

Study area

The study was conducted in the alpine grasslands of the Ordesa and Monte Perdido National Park (42°40′18″N 0°03′20″E) which is located in the Spanish Central Pyrenees and surroundings including French Pyrenees. We sampled in detail the grasslands above the local *Pinus uncinata* treeline including subalpine and alpine vegetation belts but avoiding snowbeds, screes and soil water imbibed habitats

The climate is temperate with a mild influence of the Mediterranean-type climate which becomes stronger at lower elevations. The average annual temperature and precipitation values are 4.9°C and 1650 mm respectively (at 2200 m a.s.l.: AEMET/IM 2011). Precipitation mainly occurs during autumn and spring. Snow cover lasts from October to May although the duration of the snow cover varies widely among zones as consequence of elevation and orientation. Vegetation is composed primarily of limestone rocky pastures. *Festuca gautieri* (Hackel) K. Richt. *subsp. scoparia* (Kerner ex Nyman) Kerguélen is the dominant species accompanied by a great variety of species such as creeping and cushion chamaephytes (e.g. *Astragalus sempervirens* Lam, *Sideritis hyssopifolia* L., *Androsace villosa* L or *Thymus* gr. *serpyllum* L.) and other grasses (e.g. *Koeleria vallesiana* (Honck.) Gaudinand *Helictotrichon sedenense* (DC.) Holub). The pasture-like community is always patchy and its total cover of perennial vegetation varies from 5% to 35% (Ninot et al. 2007). Low intensity cattle grazing occurs during the growing season.

Fieldwork and environmental factors

We did the surveys along the summer seasons of 2013 and 2014. We sampled 27 sites covering the whole elevational range in the territory (from 1650 to 2550 m a.s.l.)

and considering a complete range of aspects and slopes. In each site, we established a 20 m x 20 m plot representative of the surrounding vegetation avoiding rocks, screes, snow beds and humid depressions. In each plot, we placed five 2.4 m x 2.4 m quadrats, one in each corner and a fifth in the center, and recorded the cover values of each plant species within each quadrat. This sample size is adequate to include a complete representation of this type of pastures (see Pescador et al. 2015). Elevation and aspect were obtained for each plot by using a GPS (Garmin Colorado-300, Garmin Ltd., Olathe, USA) and the slope using a clinometer (Silva Clinomaster, Silva Sweden, Sollentuna, Sweden). Aspect and slope values were used to calculate Gandullo's potential solar radiation coefficient (Gandullo 1974). Two soil cores (5x10 cm) were taken within each corner-plot; one in an open area and the other under a vegetated patch. Soil of each core was air dried for one month and sieved to 2 mm. We estimated total organic carbon (C), total nitrogen (N), total phosphorus (P), potassium (K), β-glucosidase, phosphatase, soil pH and electric conductivity (EC) (for more details see López-Angulo et al. 2018). Soil fertility estimated by the multifunctionality index proposed by Maestre et al. (2012) was calculated from all the soil variables as an integrated surrogate of the ability of the each realized assemblage to sustain multiple ecosystem functions as carbon storage, productivity and buildup of nutrient pools (Maestre et al. 2012). Soil variables for the center quadrat were estimated as the average of the other four quadrats in the plot. We square-transformed soil variables and calculated weighted Z-scores for each individual soil variable and position (bare or vegetated areas) using as weights the mean cover observed for bare ground and vegetated areas in each quadrat. The multifunctionality index was the result of the average of the Z-scores of the eight soil variables (i.e. ecosystem functions) assessed.

Trait measurements

During July 2014 several plant functional traits were measured on 96 species, which represented 94% of the accumulated cover in the study area and at least 80% the plant cover for each quadrat, which is representative enough of the functional composition of the local plant communities (Pakeman et al. 2007). For each species, we measured 5 traits on 10 random individuals recorded in the site where each species was more abundant. The selected traits were plant vegetative maximum height (Hmax), leaf dry matter content (LDMC), specific leaf area (SLA), leaf thickness (LT) and seed mass (SM). According to the leaf-height-seed (LHS) plant ecology strategy scheme proposed by Westoby (1998), these five traits reflect key plant ecological strategies. Traits were measured following the protocols outlined in Cornelissen et al. (2003). In some rare cases some traits were impossible to measure in the field. In these cases, we completed our trait database with information from the Royal Botanic Gardens Kew Seed Information Database (SID) (Flynn et al. 2008) and from the LEDA traits database (Kleyer et al. 2008) (0.3% of entries and 0.02% of the cumulated cover for the whole community). Trait data from some species (0.08% of entries and 0.1% of the cumulated cover for the whole community) were inferred from congeneric information on the mentioned databases.

Functional diversity

Traits were log-transformed when necessary to attain normality. To estimate functional distances among species, we computed the Gower distance between their trait mean values, using the function *gowdis* in the *FD* package for R v 3.3.3 (R Core Team 2016). We computed Gower distances per each single-trait and for the ensemble of traits (i.e. "multi-trait"). To estimate functional diversity (for each trait and for all traits together) in each community we computed the weighted mean pairwise distance (MPD) (i.e.,

weighted by the relative cover of each species in each community). MPD was computed using the *mpd* function in the package *picante* (Kembel et al. 2010). This index is independent from the number of species and it is highly correlated with other widely used indices of functional diversity (de Bello et al. 2016)... MPD was calculated also for each null assemblage generated.

Null models of community assembly

Our null model framework involved three main steps: 1) fit statistical models of abundance in each plot (i.e., cover) for each species; 2) fit different models of occurrence (i.e., probability of occurrence) in each plot per each species; and 3) build null communities combining predictions from models 2 and 1.

Models of species abundance. We first performed a principal component analysis (PCA) on 11 environmental variables (the eight soil variables, together with elevation, slope and potential solar radiation) using function *princomp* in package *stats* (Oksanen et al, 2017). Then, we fitted linear models (with Gaussian errors) to species abundance (i.e., cover) using the first five PCA axes, their quadratic terms and all interaction terms as explanatory variables. The standard model checking showed these to be acceptable models and therefore any transformation was need. The model checking didn't show any problematic pattern. A stepwise variable-selection procedure based on AIC was used to find the best predictive model for each species. Linear models and stepwise selection were performed with functions *glm* of the package *stats* and *stepAIC* of the package *MASS* in R (R Core Team 2016).

Models of species occurrence. As already commented in the Introduction, we employed three different strategies to model species occurrence: abiotic, biotic and mixed abiotic-biotic:

For the so-called abiotic null model, we modeled species distribution according only to abiotic environmental variables. We fitted generalized linear models (with binomial error distribution and using a logit link function) to species occurrence (i.e., presence/absence) using the first five PCA axes, their quadratic terms and all interaction terms as explanatory variables. A stepwise variable-selection procedure based on AIC was used to find the best predictive model for each species.

To fit biotic models, we used the Beals' smoothing (Beals 1984; De Cáceres & Legendre 2008). This method estimates the probability of occurrence of some target species in a quadrat according to the observed species composition and the pattern of species co-occurrence of the target species with other species in the whole community. Thus, the probability that a given target species j occurs in a quadrat i is defined as:

$$p_{ij} = (1/S_i) \sum_{k=1}^{s} \frac{m_{jk} x_{ik}}{n_k},$$

where S_i is the number of species in quadrat i, m_{jk} the number of joint occurrences of species j and k, n_k the number of occurrences of species k in the community matrix and x_{ik} is the incidence (0 or 1) of species k in quadrat i and s is the number of different species in the community (De Cáceres & Legendre 2008). Beals smoothing was performed with function beals of package vegan (Oksanen et al. 2013).

Finally, we fitted mixed abiotic-biotic models in which we modeled species occurrence according to abiotic environment and the pattern of species co-occurrence simultaneously using latent variable models (LVM; Skrondal & Rabe-Hesketh 2004; Bartholomew et al. 2011). A LVM is a function (similar to a GLM) fitted to both observed and non-observed (i.e., latent variables) predictors. The latent variables

account for any residual covariation not explained by the environmental conditions, including the residual correlation between species (Warton et al. 2015).

One way of defining a LVM for binomial data would be, for example:

$$probit(p_{ij}) = \alpha_i + \beta_{0j} + \boldsymbol{x}_i' \beta_j + u_{ij}$$

where p_{ij} is the probability of finding species j in sample i; β_{0j} is an intercept, β_j is a vector of regression coefficients, $\boldsymbol{x}_i'$ is the transposed vector of environmental predictors measured in sample i and u_{ij} is a random effect defined as a function of latent variables $\boldsymbol{z}_i$ and factor loadings λ_j, i.e., as $u_{ij} = \boldsymbol{z}_i' \lambda_j$ (Warton et al. 2015). Latent variables have been considered as quantities that mediate interactions between taxa (i.e., "interaction currencies", Kissling et al. 2012; D'Amen et al. 2017).

We fitted LVM's to species incidences (i.e., as binomial response) based on the five PCAs and their quadratic terms (as observed predictors) and two latent variables, using probit as the link function. These analyses were implemented with the function *boral* of the package *boral* (Hui 2016).

Building null communities. For each of our null model strategies (i.e., abiotic, biotic and mixed abiotic-biotic), we combined predictions from the respective fitted model of species occurrence and the fitted model of species abundance within a bootstrap framework. In each simulation, the number of species in each quadrat was held identical to those found in the observed communities. We generated 999 null assemblages per quadrat and per null model.

Statistical analyses

For each quadrat, we calculated the standardized effect size (SES: Gotelli & McCabe 2002) of functional diversity [i.e., $SES = MPD_{obs} - \overline{MPD}_{sim}/sd\,(MPD_{sim})$] for each functional trait independently and for all the traits together (hereafter "multi-trait FD").

To evaluate whether the relative strength of abiotic or biotic mechanisms of community functional structure, i.e., the discrepancies between observed and expected functional diversity estimated as the SES values, varied along stress gradients, we fitted linear mixed models (Pinheiro & Bates 2000) based on elevation, potential solar radiation and soil fertility. We included also the quadratic term of elevation as a fixed effect and considered plot as random effects. We checked for collinearity between the different environmental predictors using the variance inflation factor (VIF) before building the models. In all cases were below 2, suggesting the absence of collinearity problems (Chatterjee & Hadi 2001). Normality of standardized residuals was visually checked for all the models. We estimated the statistical significance of each predictor using a type-II analysis of variance.

Results

We registered 159 species in the 135 quadrats sampled (27 plots). Species richness per quadrat varied from 4 to 42 with a mean value of 18.8. The most abundant species together with the *Festuca gautieri subsp. scoparia* were other graminoids such as *Koeleria vallesiana* (Honck.) Gaudin subsp. *vallesiana* and *Helictotrichon sedenense* (DC.) Holub and some creeping chamaephytes such as *Thymus* gr. *serpyllum* L. and *Galium pyrenaicum* Gouan. These last species had similar incidence frequencies (number of occurrences) to graminoids but their covers were lower. About half of the recorded species occurred only in less than a 5% of the quadrats (less than six

occurrences). The rest of species occurred at least in a 20% of the quadrats (135), being 115 (89%) the maximum occurrence per a species (*Thymus* gr. *serpyllum* L.).

Our three models were able to reproduce realistically the observed functional structures with a notable reduced number of significant deviations. Overall, the observed functional diversity was not significantly different from expected, independently of the trait analyzed and the null model employed (Table 1). The percentage observed of quadrats where observed FD significantly differed from expected FD varied from 0% to a low 6.66%. The larger number of deviant quadrats was found for SLA under the abiotic null model.

Table 1. Number of quadrats that observed FD was significantly different from expected FD under the null models (-1.96 < SES > 1.96) in 135 quadrats.

Null model	Trait					
	SM	SLA	LDMC	LT	Hmax	Multi-trait
Abiotic	0	9	0	2	0	0
Biotic	0	4	4	1	1	4
Mix[*]	1	2	4	6	3	4

*Mix: mixed abiotic-biotic null model

In any case, we found differences among null models in their ability to reproduce some properties of the studied communities. For instance, the biotic and mixed null models quite faithfully reproduced the frequency of apparition of each species (Fig. 1). On the contrary, the expected frequency of species under the abiotic null model was mostly similar to the expected frequency if they had entered the null communities randomly (i.e., with a frequency equal to the ratio between total incidence and the total number of species; Fig. 1, Appendix 1). Only for some species there was a linear relationship between the expected and the observed frequencies and, in any case, the expected was always lower than the observed.

Figure 1. Relationship between the observed frequency of each specie and its expected frequency (average of 999 randomizations) estimated under the abiotic null model (red points), the biotic null model (gray points) and the mixed abiotic-biotic null model (black points) in the total sample. Black lines represent the expected value if all species entry randomly (the ratio between total incidence and the number of species, i.e., ~16 occurrences).
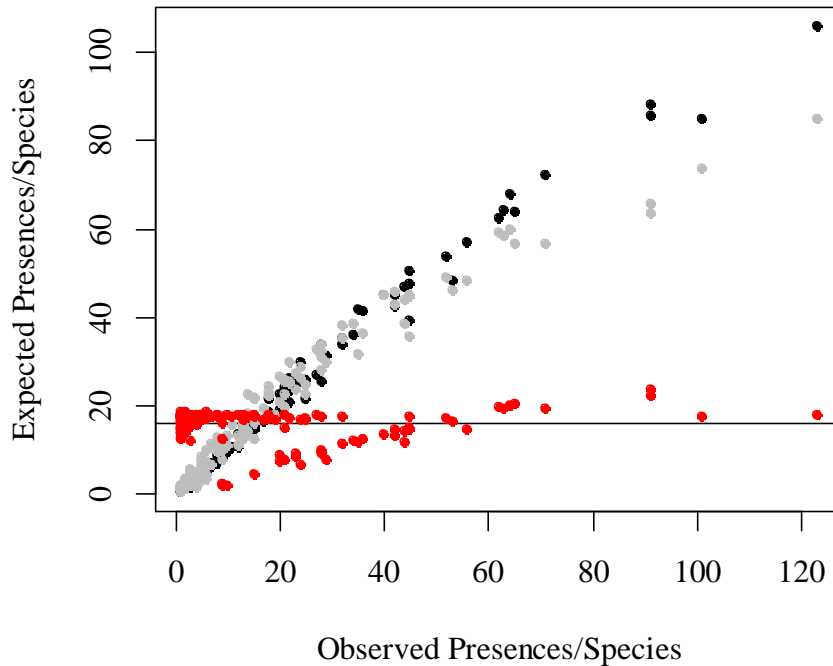
Discrepancies between observed and expected functional diversity estimated as the SES values (termed FD henceforth) for all functional traits including the multi-trait combo except SLA and LDMC were related to some environmental predictor in the case of the abiotic null model (Table 1). Specifically, we found a significant positive effect of elevation (i.e., a tendency to FD being larger than expected as elevation increased) on the FD of maximum plant height and multi-trait combo, a significant positive effect of the squared term of elevation over FD for leaf thickness and a significant negative effect of potential solar radiation over FD of maximum plant height and seed mass. In the case of the biotic null model, we found only a positive significant effect of elevation over the FD of maximum plant height. On the contrary, no significant

effect of any environmental predictor was found for any of the SES from the mixed abioic-biotic null model (Table 2, Fig. 2). Besides, we did not detect any significant effect of soil fertility in functional structure and, functional diversity in SLA and LDMC were not influenced by any abiotic factor.

Figure 2. Responses of different metrics of functional diversity to potential solar radiation and elevational gradient. Only significant relationships are showed. The fitted lines indicate results from LMMs with confidence intervals. Results from a) to e) were obtained under Abiotic null model and f) under Biotic null model.
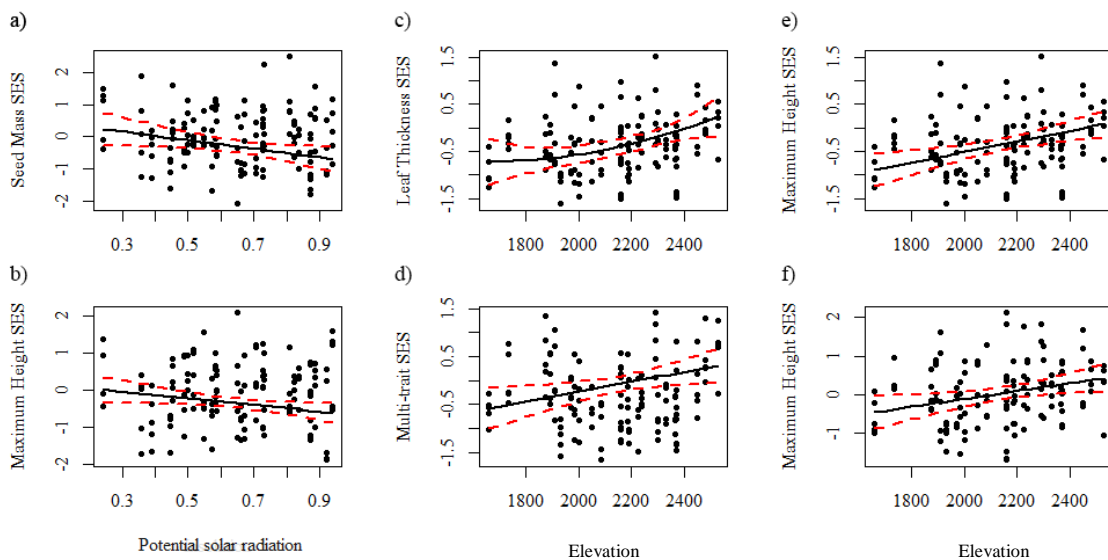
Discussion

Here, we used a novel approach for incorporating abiotic and biotic determinants (*i.e.* ecological assembly rules) into null models to reveal the role played by two critical deterministic processes, abiotic conditions and biotic interactions in the community assembly. Comparisons between the functional structure of observed assemblages and the functional structure expected under the effect of abiotic, biotic or both mechanisms assembly rules, allows us to infer whether these two critical ecological forces individually or simultaneously determine the community assembly and if so, their relative prevalence along the environmental gradients. Although all our three realistic

null models are able to reproduce the functional structure for the multi-trait but also for all the considered individual plant traits, their performance varied along the environmental gradients considered.

Table 2 Coefficients of the linear mixed effect models (LMMs) examining the effects of environmental gradients on the SES of the FD (discrepancies between observed and expected FD values) for each null model considered. Only results for models with significant effects are shown.

	Abiotic model		Biotic model		Mixed abiotic-biotic model
Seed mass					
intercept	-0.31				
potential solar radiation	-0.25	*			
elevation	0.19				
soil fertility	0.10				
Maximum plant height					
intercept	-0.353		0.04		
potential solar radiation	-0.168	**	-0.12		
elevation	0.251	*	0.23	*	
soil fertility	0.098		0.02		
Leaf Thickness					
intercept	0.282				
potential solar radiation	-0.109				
elevation^2	0.148	*			
elevation	0.114	*			
soil fertility	0.084				
Multi-trait					
intercept	-0.083				
potential solar radiation	-0.158				
elevation	0.228	*			
soil fertility	0.063				

elevation^2: the quadratic term of elevation. The significance is shown as ** $P<0.005$, * $P<0.05$.

Overall, our results showed that the number of quadrats where the percentage of FD was lower than expected were almost inexistent for all the considered null models and traits indicating that the null model algorithms accurately described functional community assembly (Table 1). A preliminary consideration of the functioning of this species-rich high mountain grassland of Central Pyrenees would suggest that the abiotic and biotic rules would be similarly important in structuring the functional configuration of the communities. However, when evaluating the performance of the null models, we found important differences. For instance, whereas the frequencies of species occurrence generated under the biotic and mixed abiotic-biotic null models were very similar to the observed in the community matrix, the ones generated under the abiotic null models were quite different (Fig. 1). In this last case, we found a group of species, which corresponds to those more frequents, whose frequencies of occurrence tended to be proportional to the observed frequencies, whereas rare species (i.e., species present in less than 20% quadrats) appeared in the null assemblages with the frequency which they would had in a unweighted random assembly, which is by far larger than observed.

In addition, the abiotic null model was also the worst null model reproducing the composition of assemblages (Appendix 1), suggesting that the abiotic processes themselves are unable to completely explain the observed patterns, and thus, other processes such as biotic interactions are necessary to better reproduce the community functional configuration (Cornwell & Ackerly 2009; de Bello et al. 2012). In fact, when analyzing the relationships among the SES of FD for each single-trait and multi-trait along conspicuous environmental gradients, we detected significant relationships with the environmental gradients with the abiotic null model (Fig 2). Specifically, the largest FDs in absolute values were found at both edges of the elevational and solar radiation

gradients. This result suggests that the biotic interactions can be much more important in these parts of the gradients (Michalet et al. 2006) which are by far much stressful.

Worth to note that an increase in potential solar radiation led from functional divergence to convergence in plant height and seed mass was found. Solar radiation is a proxy for energy input, which may negatively affect the performance of alpine plant species in terms of water balance and evapotranspiration (Mooney et al. 1965; Ritchie 1998). However, in the alpine systems as the Central Pyrenees as in others temperate mountains where summer storms are frequent, solar radiation seems to exert a positive effect by lengthening of the effective growing season through early snowmelt (Körner 2003). Previous studies in similar systems have also detected a tendency to convergence in seed mass with increasing solar radiation (de Bello et al. 2013), and even convergence in plant height in early snowmelt zones (Venn et al. 2011). In our case, the patterns of convergence in plant height and seed mass should not be mediated by abiotic conditions because the null communities were generated with a mechanistic model with parameters that specify abiotic processes (Chalmandrier et al. 2013; Botta-Dukát & Czúcz 2016). Our results support the idea that in more relatively benign conditions trait convergence patterns can be due to competitive processes, which sort species with different competitive abilities (*i.e.* exclude less stress-tolerant species) (Mayfield & Levine 2010). It is worth noting that the grasslands belonging to the *Festucion scopariae* alliance have preference for sites with the highest solar radiation (Alonso 2005), whereas in other less insolated localities, it is probably that the competitive ability of the species that dominate the community is avoided for other plants, functionally dissimilar which may enter the community.

Functional divergence of maximum plant height, leaf thickness and multi-trait variability increased with elevation (Fig. 2). Mechanisms that induce greater functional dispersion are associated in the literature to two opposite processes, competition (MacArthur & Levins 1967) or facilitation (Soliveres et al. 2012; Gross et al. 2013). The 'stress-gradient hypothesis' suggest that facilitation will become prevalent over competition as environmental stress increases (Michalet et al. 2006) and therefore, facilitative processes are expected to increase with elevation due to extreme environmental conditions (Callaway et al. 2002; Chalmandrier et al. 2017).In addition, we found the same effect of elevation on maximum plant height FD using the biotic null model (Fig 3). This result suggests that the variation from functional convergence to functional divergence along the elevational gradient should not only caused by biotic mechanisms, but also by abiotic factors. However, there are many possible interpretations of this result because there are many possible geophysical drivers related to elevational gradients, as summarized in Körner (2007). Another possible explanation for this pattern may involve the effects of disturbance regimes on trait variation, in particular cattle grazing whose intensity increase at low elevations. Thus, species that lack traits for persisting under grazing conditions would be removed from community (Díaz et al. 2001; de Bello et al. 2006; Ding et al. 2012) decreasing functional diversity. In fact, hemicryptophytes, the dominant plants in intensively grasslands share similar plant sizes.

In the last two decades, ecologists have become increasingly interested in finding ways to reveal the processes driving community assembly from the functional ecology perspective, but no consensus has been reached regarding which is the most appropriate protocol that is used to generate the null communities (Gotelli & Graves 1996). We provide some insights on new theoretical and methodological advances in

null model analysis for the assessment of the relative importance of processes and mechanisms underlying community assembly. Our approach reveled the importance of using appropriate null models with clear connection with ecological driven processes for successfully detecting the underlying mechanisms that shape the functional structure of the plant communities (de Bello 2012).

Generating null assemblages under the action of a particular ecological assembly rule allows comparing observed and expected patterns and to decide if the observed communities are compatible with such an ecological rule. Specifically, our results highlight the potential of the environmentally constrained null models to test for the effect of biotic interactions such as facilitation or competition. Thus, our results indicate that biotic interactions are critical driver of community assembly in alpine ecosystems while species sorting due to environmental processes appear to play a relatively weaker role at least at fine spatial resolutions such as those considered in this study.

In this context, we would like to highlight two important caveats for future studies: (1) it is important to emphasize the utility of null models to compare patterns but attention must be paid to infer community assembly mechanisms because different processes could give same results (Kraft et al. 2015) (2) We fixed species richness at each site in our null models, assuming that the carrying capacity of each site is different in function of the local ecological conditions, such as soil fertility and abiotic stress. Therefore, the detection of biotic processes could become blurred since species richness is also an outcome of competitive interactions. We hope to inspire further studies that will contribute to build a unifying methodological framework for functional ecology analysis.

Acknowledgements

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Appendix 1. Incidence matrix representations of (a) the original data, and the data generate under the (b) Abiotic, (c) Biotic, and (d) Mix null models. The intensity of the color indicates the incidence for the average of 999 randomizations except for the original data that are a presence/absence matrix.
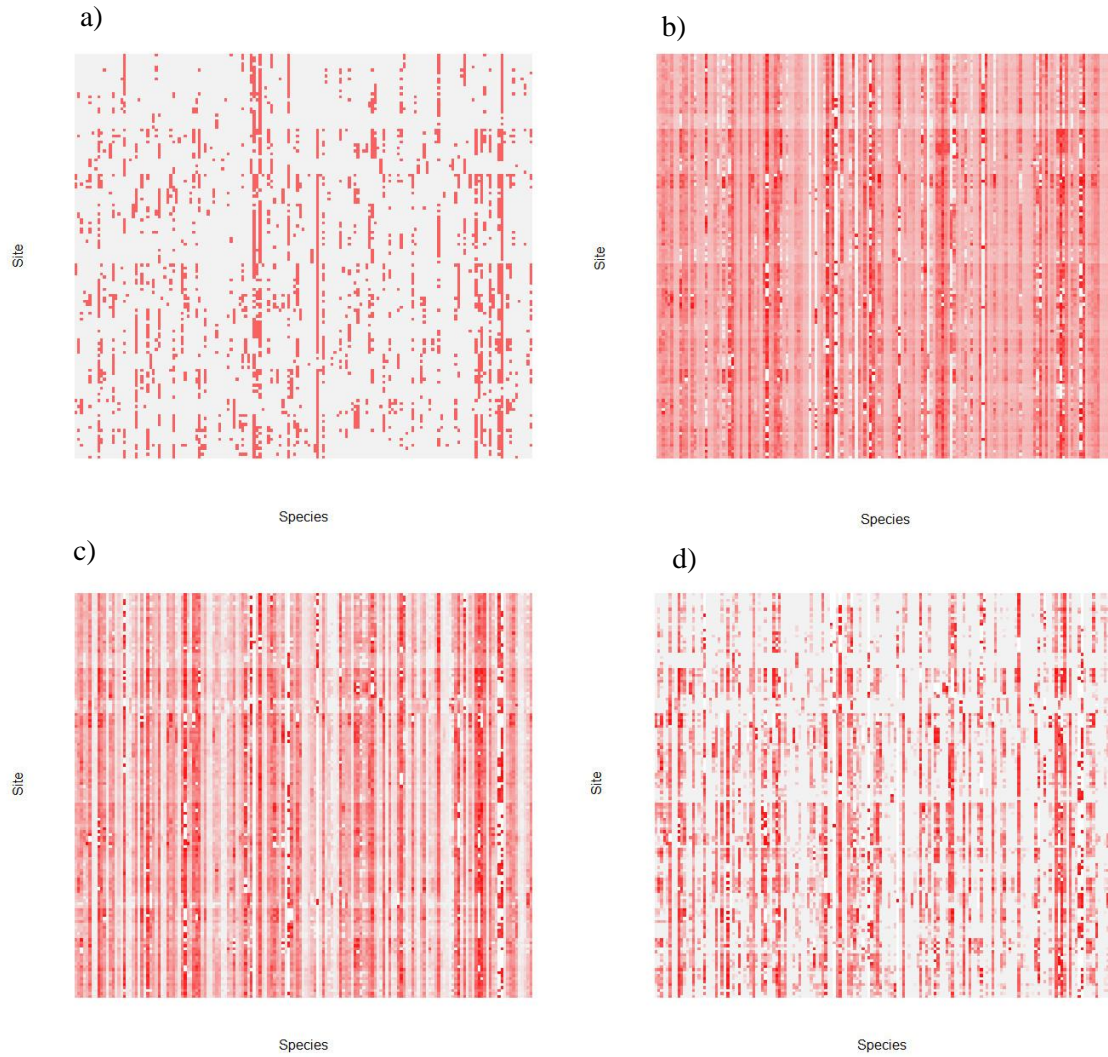
Capítulo 4

Biogeography and climatic context determine the interplay among functional, phylogenetic and taxonomic diversity with the abiotic and biotic environments

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Abstract

Abiotic conditions and plant to plant interactions are critical determinants in shaping distribution of the diversity components at fine scales. We assessed the interplay between taxonomic (TD), functional (FD), and phylogenetic diversity (PD) in natural assemblages may help to identify the assembly mechanisms that lead local communities. The regional species pool originated by historical processes together with the climatic context and man-driven perturbations will determine the relationships between the environment and the community structure

 Although harsh alpine environment generally produces convergence in community assembly processes throughout the world's mountains even in geographically distant regions (e.g. facilitation: Callaway et al. 2002), intrinsic and local characteristics such as climate and evolutionary history, can alter the prevalence of these processes (Safi et al. 2011). Thus,. Although thus far, few studies having addressed the relationships between PD, FD and TD, and their biotic and abiotic determinants (but see: Bernard-Verdier et al. 2013; Oliver et al. 2013; Dainese et al. 2015), results for most studies may be frankly idiosyncratic and limit the search for general principles underlying processes structuring plant communities. Therefore, to progress toward a unified framework, we need to assess the interplay of PD, FD and TD and their environment in a unique ecosystem (alpine ecosystem) but in different mountain ranges with a completely different evolutionary and biogeographic histories (Europe/South America) and with patent different climatic conditions (Mediterranean and Eurosiberian regions) within the same biogeographical region.

 Here, we propose a causal framework to determine how several key abiotic and biotic determinants -elevation, total nitrogen in soil, potential solar radiation and biotic

interactions at the local assemblage level (C-score: Stone & Roberts 1990; Dullinger et al. 2007) shape the relationships among TD, FD and PD. Furthermore, to know if the causal relationships affect the origin and maintenance of TD in different mountains with distinct regional species pools constrained by different rates of trait evolution and speciation, and different climatic conditions, we compare the interplay between FD, PD and TD in three different mountain ranges controlling the evolutionary history and the climatic conditions.

Introduction

Disentangling underlying mechanisms driving the assembly of plant species in natural communities is critical for understanding the uneven distribution of species diversity across the earth (Diamond 1975; Keddy & Weiher 1999; Gotelli & McCabe 2002). It is well known that plant species are not distributed randomly, but abiotic conditions and plant to plant interactions are critical in determining species co-occurrence at fine scales and species composition in natural communities (Keddy 1992; Chase & Myers 2011; HilleRisLambers et al. 2012). The functional perspective of the community assembly suggests that biotic and abiotic determinants could act as ecological filters allowing species to enter into the community on the basis of their functional trait configuration (Cornwell & Ackerly 2009; Götzenberger et al. 2012). This implies that only those species with the appropriate morphological, physiological, and phenological traits will be able at least in probabilistic terms to enter into the natural assemblages and persist successfully through time (Violle et al. 2007; Shipley et al. 2016). This plant trait-based framework have led over the last decades to a need of incorporating functional information in the studies of community assembly and lately the explicit consideration of the phylogenetic structure of the assemblages since most of the critical functional traits have a patent evolutionary signal (Diaz et al. 1998; Webb et al. 2002; Pavoine & Bonsall 2011; Escudero & Valladares 2016).

Traditionally, species richness and individual abundance distributions have been used to detect community assembly processes by using null models of known numerical properties (Rosenzweig 1995; Grytnes & Vetaas 2002; Willig et al. 2003). However, this perspective assumes that species are ecologically equivalent and evolutionary independent (Safi et al. 2011; Swenson 2011). So, entrance of functional and

phylogenetic perspectives would facilitate the inclusion of the ecological and evolutionary information about species overcoming the inherent limitations of the so-called taxonomic approach. Combining the distributions of species, their level of co-occurrence and their functional similarity would allow to identify assembly rules or other ecological processes that taken together would determine the composition of communities (Weiher & Keddy 1995; Diaz et al. 1998). In addition, the use of the phylogenetic relatedness between species is also leading the explicit consideration of the historical processes underlying speciation and other events such as species diversification or migration in the assembly process (Davis et al. 2002; Webb et al. 2002; Hughes & Eastwood 2006). Furthermore, the quantification of the phylogenetic relationship among species has given information related to local-scale ecological processes under the premise that closely related species are more ecologically similar (Webb et al. 2002; Hardy 2008; Mayfield & Levine 2010; Le Bagousse-Pinguet et al. 2017).

Assessing the relationships between these three components of diversity in natural assemblages, functional diversity (FD), phylogenetic diversity (PD) and taxonomic diversity (TD), may help to identify the mechanisms that lead local communities (Pavoine & Bonsall 2011; Oliver et al. 2013; Dainese et al. 2015). Plant trait-based ecology (Escudero & Valladares 2016; Shipley et al. 2016) suggests that a strong correlation between FD and TD is expected when species functional uniqueness predominates in species traits (equally complementary: Petchey & Gaston 2002). This means that there were almost no functional redundancy between species, so each taxonomic label (i.e. species name) would correspond to a unique functional configuration. The emergence of these correlations between these two diversities might reflect the importance of niche complementarity as mechanism of community assembly.

However, low levels of functional diversity relative to high levels of TD might suggest environmental filtering (Keddy 1992; Kraft & Ackerly 2010). On the other hand, the relationships between FD and PD will be structured according to the phylogenetic signal of the functional traits implied. That is to say, that high FD values could lead high PD values if phylogenetic conservatism prevails in the functional traits selected to estimate FD (Webb et al. 2002). If the measured traits are not critical for the assembly but other unmeasured aspects of plant functioning in the community with phylogenetic signal, PD would be structured according to deterministic forces operating on those unmeasured attributes.

Disentangling the variation of the interplay between FD, PD and TD along biotic and abiotic gradients would provide insights into community assembly processes because the responses of the different components of diversity, TD,FD and PD, to environmental changes underlie variation in resource requirements and environmental tolerances of the species (Pavoine & Bonsall 2011; Oliver et al. 2013; Dainese et al. 2015). Mountains ecosystems are excellent candidates to evaluate the relationships between these three facets of diversity and for understanding variation in the assembly processes along environmental gradients due to the strong and foreseeable environmental changes that are produced with elevation, a surrogate of climatic variations (Körner 2007; Sanders & Rahbek 2012). Even more, recent information suggests that variations in elevation and other secondary abiotic variables such as solar radiation, have important consequences in the structuration not only of the TD but the other two, FD and PD. For instance, elevation yields environmental filtering constraining FD (de Bello et al. 2013; Read et al. 2014), PD (Jin et al. 2015; Xu et al. 2017) and TD (Rahbek 1995; Cuesta et al. 2017) although other relationships have been also found (Le Bagousse-Pinguet et al. 2017; López-Angulo et al. 2018). There are

other critical abiotic determinants in high mountain environments such as total nitrogen in the soil, considered as the main limiting nutrient in alpine ecosystems (Sundqvist et al. 2014) and solar radiation (de Bello et al. 2013), which can generate microheterogeneity at fine scales modifying the climatic primary conditions (i.e. temperature) produced by elevation. Besides, biotic interactions, especially positive ones, are known for playing a key role in the processes governing community assembly in high-mountains (Choler et al. 2001; Callaway 2007; Cavieres et al. 2014) leaving also detectable imprints on the functional and phylogenetic structure of the natural communities (Verdú & Valiente-Banuet 2011).

Although harsh alpine environment generally produces convergence in community assembly processes throughout the world's mountains even in geographically distant regions (e.g. facilitation: Callaway et al. 2002), intrinsic and local characteristics such as climate and evolutionary history, can alter the prevalence of these processes (Safi et al. 2011). Thus, the regional species pool originated by historical factors related to biogeographical and evolutionary processes together with the climatic context and man-driven perturbations will determine the relationships between the environment and the community structure including the floristic composition, and as well as the interplay of the different components of diversity. Although thus far, few studies having addressed the relationships between PD, FD and TD, and their biotic and abiotic determinants (but see: Bernard-Verdier et al. 2013; Oliver et al. 2013; Dainese et al. 2015), results for most studies may be frankly idiosyncratic and limit the search for general principles underlying processes structuring plant communities. Therefore, to progress toward a unified framework, we need to assess the interplay of PD, FD and TD and their environment in a unique ecosystem (alpine ecosystem) but in different mountain ranges with a completely different

evolutionary and biogeographic histories (Europe/South America) and with patent different climatic conditions (Mediterranean and Eurosiberian regions) within the same biogeographical region.

Here, we propose a causal framework to determine how several key abiotic and biotic determinants -elevation, total nitrogen in soil, potential solar radiation and biotic interactions at the local assemblage level (C-score: Stone & Roberts 1990; Dullinger et al. 2007) shape the relationships among TD, FD and PD. Furthermore, to know if the causal relationships affect the origin and maintenance of TD in different mountains with distinct regional species pools constrained by different rates of trait evolution and speciation, and different climatic conditions, we compare the interplay between FD, PD and TD in three different mountain ranges controlling the evolutionary history and the climatic conditions.

Materials and Methods

Study sites

This study was conducted at three mountain ranges, with different climate and/or distinct biogeographical history (Table 1). (1) The Sierra de Guadarrama National Park (40°47' N, 4°0' W), in central Spain, which is characterized by a typical Mediterranean climate; (2) The Ordesa-Monte Perdido National Park (42°40′ N 0°03′ E), within the same geographic region but with a flora belonging mainly to the Eurosiberian region (in the north fringe of the Iberian Peninsula), and consequently characterized by a temperate climate; and (3) the surroundings of the Valle Nevado (33°20'S, 70°14'W) and the Laguna del Maule (35°58'S, 70°30'W), in the central Chilean Andes, with a completely different regional species pool but also characterized by a Mediterranean-

type climate which is characterized by a marked seasonality and intense summer drought becoming more pronounced at lower elevations. Mean annual temperature and annual precipitation are 6.5 ºC and 1350 mm at 1894 m a.s.l. (Navacerrada Pass weather station; 40° 470 N, 4° 00 W; 1894 m a.s.l.) respectively, in the Guadarrama NP. In the central Chilean Andes, the mean annual temperature and annual precipitation are 6.5 ºC (Cavieres et al. 2000) and 943 mm (Santibañez & Uribe 1990) respectively, at 2300 m a.s.l.. Finally, the Ordesa-Monte Perdido NP has a temperate climate without a summer drought since storms in summer are very frequent. Mean annual temperature and annual precipitation are 5ºC and 1660 mm (Góriz weather Station; 42º 39' N, 00º 01' E; 2215 m a.s.l.) respectively, being Ordesa-Monte Perdido NP the wettest and coldest site.

Table 1. Mean and standard deviation values of the endogenous and exogenous variables included in the structural equation model.

Mountain range	SP	PD	FD	C-score	Elevation	Potential solar radiation	Soil total nitrogen (mg g^{-1})
Guadarrama NP	11	0,373	0,303	46,10	2127	0,739	3,710
Ordesa-Monte Perdido NP	19	0,363	0,219	47,15	2144	0,649	3,279
Central Mediterranean Andes	11	0,348	0,270	40,08	2834 *(884)	0,814	0,616

*Standardized elevation is shown in parentheses.

At each mountain region, we sampled the grasslands occurring above the local treeline in snow-free zones such as windblown slopes and crests covering the complete elevational gradient where this ecosystem-type occurs. The elevation in our study ranges from 1890 to 2420 m in Guadarrama NP, from 1650 to 2550 m in Ordesa-Monte Perdido NP, and from 2064 to 3627 m a.s.l. in the in the central Chilean Andes. The

dominant perennial vegetation in the three locations is generally patchy with bare ground areas and it comprises grasses manly belonging to the genus *Festuca* and *Poa,* accompanied by other growth forms such as creeping chamaephytes, perennial forbs and cushion-like plants.

Field sampling

We sampled 39 sites during July and August of 2011 in Guadarrama NP, 27 sites during July of 2013 in Ordesa-Monte Perdido NP, and 20 sites during January of 2014 in the central Mediterranean Andes. We established in each site a sampling plot of 20 x 20 m in relatively homogeneous vegetated areas considering a wide range of aspects and slopes along the local elevational gradient. Five 2.4 m x 2.4 m quadrats were established at the four-corners of the plot and a fifth in the center. This sample size has been showed to be large enough to represent the variation of this type of communities (see Pescador et al. 2015). The central quadrat was thoroughly divided into 64 cells of 30 cm x 30 cm (8 x 8 cells). The percentage cover in percentage per species was visually estimated at each quadrat and each cell. Quadrat information was used to calculate the diversity metrics described below. Cell information was used to calculate the checkerboard score (C-score: Stone & Roberts 1990) with the aim of incorporating an estimate of the type and strength of spatial plant to plant interactions (Dullinger et al. 2007). The C-score index quantifies the degree of aggregation for species co-occurrence. High C-score values indicate a tendency for species to segregate spatially which mainly corresponds to competitive interactions leading co-occurrence patterns, and low values would indicate species aggregation and facilitative processes (Dullinger et al. 2007). We used a grid size of 30 cm x 30 cm because the average diameter of the plant species was of 18 cm for Guadarrama NP and central Mediterranean Andes and 6

cm for Ordesa-Monte Perdido NP (authors' own unpublished data) which would reflect the real plant to plant interactions in the observed assemblage.

We measured in each plot the elevation and aspect using a GPS (Garmin Colorado-300, Garmin Ltd., Olathe, USA) and the slope using a clinometer (Silva Clinomaster, Silva Sweden, Sollentuna, Sweden). Aspect and slope values were used to calculate the potential solar radiation (Gandullo 1974). Elevation was standardized by subtracting the treeline elevation from plot elevation in the Chilean Andes (see: López-Angulo et al. 2018) since the sampled sites were distributed in different latitudes and the treeline was locally well-conserved. We collected one soil sample (5 cm in diameter and 10 cm deep) at the four corners of each plot in bare areas since soils in vegetated patches are very homogeneous in all these systems whereas bare ground areas reflect the variations linked to abiotic differences among sites (Mihoč et al. 2016). The soil estimates of center quadrat were estimated as the average of the four quadrats at each site. Soil samples were air dried for one month and sieved through a 2 mm mesh. We measured soil total nitrogen because is considered one of the main limiting nutrients in alpine ecosystems (Sundqvist et al. 2014). Soil total nitrogen (mg N g-1 soil) was determined on a SKALAR++ San Analyzer (Skalar, Breda, The Netherlands) in the Nutrilab/URJC lab after digestion with sulphuric acid and Kjedahl´s catalyst (Anderson & Ingram 1994).

Plant Functional Traits

Five functional traits were measured for the most abundant species in each mountain range (56 species (98%) of the total) in Guadarrama NP, 96 (60%) species in Ordesa-Monte Perdido NP and 71 (67%) species in in the central Chilean Andes). These groups of species represented at least 80% of the accumulated cover of each quadrat

(Borgy et al. 2017) reaching 99% of the accumulated cover in Guadarrama NP, 0.94% in Ordesa-Monte Perdido NP and 87% in Central Chile. We measured five key functional traits that are expected to play a critical role in the functional niche differentiation between species. (i) Maximum vegetative height (Hmax, distance from the ground to the top of photosynthetic tissues) is correlated with above-ground biomass and represents a trade-off between competitive vigor (Cornelissen et al. 2003) and protection by snow cover (Körner 2003). (ii) Plant size (SI, canopy area projection) is as surrogate of the photosynthetic biomass and is related to accumulated resources (Pescador et al. 2015). (iii) Specific leaf area (SLA, ratio of one-sided area of a fresh leaf divided by its dry mass) is correlated with relative growth and photosynthetic rates (Cornelissen et al. 2003). (iv) Leaf dry matter content (LDMC, oven-dried mass of a leaf divided by its fresh water-saturated leaf mass) is usually well correlated with investment in leaf tissues resistance to physical hazards (Cornelissen et al. 2003). (v) Leaf thickness (LT) is related to nutrient acquisition and resistance to wind (Choler 2005). All these traits were measured on at least ten different healthy and well developed individuals per species, following the standard methodology of Cornelissen et al. (2003) with the exception of plant size (SI), which was calculated as $SI = \pi \cdot L \cdot S/4$ (Pescador et al. 2015), where L is the longest diameter and S is the shorter diameter perpendicular to the former one. In addition, trait data for the Ordesa-Monte Perdido NP was completed with information from the LEDA traits database (Kleyer et al. 2008).

DNA sequencing and phylogenetic analysis

We constructed a phylogenetic tree using two barcoding loci (rbcL and matK) in order to estimate the phylogenetic diversity. We used a species pool composed by species found in the communities together with similar ecosystem species from Torres

del Paine NP (Chile). Available species sequences from GenBank were downloaded (122 matK and 117 rbcL sequences) and the rest of them (771 sequences) were obtained in the laboratory. Fresh leaves from three individuals per species were collected and were lately dry-stored in silica-gel for 1 month. Genomic DNA was isolated and extracted using the DNeasy Plant Mini Kit (QIAGEN, Valencia, CA, USA).

PCR amplifications of the rbcL barcode were performed in 25 µL containing a reaction mixture of 2.5 µL of Taq buffer 2 mM with MgCl2, 1 µL of dNTP Mix (0.4 mM), 1.25 µL of reverse and forward primer, 1.25 U Taq DNA Polymerase (Biotools, Madrid, Spain) and 2 µL of genomic DNA. The matK barcode was amplified by puReTaq Ready-To-Go PCR beads (Amersham Pharmacia Biotech, Uppsala, Sweden). Primers for PCR, sequencing and PCR cycling conditions used in this study follow (Lopez-Angulo et. in press). The subsequent products were clean-up using the ExoSap purification kit® (USB Corporation, Cleveland, OH, USA) and sequenced by Macrogen Inc (Seoul, South Korea). Sequences were initially aligned using MAFFT online v. 7, and minor manual adjustment of the alignments was necessary only for the matK barcoding with Mesquite version 2.6. Maximum likelihood (ML) gene trees were calculated by the R-package Phangorn (Schliep 2011) using the GTR+G+I model and 100 bootstrap replicates.

Diversity metrics and statistical analyses

We used the species richness as measure of TD, and the mean pairwise distance (MPD) weighted by species abundances to estimate the functional and phylogenetic structure. The distances among the coexisting species were calculated using the Gower distance to estimate FD and the cophenetic distance to estimate de PD. Before calculating the FD, we conducted a principal component analysis (PCA) using all the

traits measured to control the correlation among traits and to defined an multidimensional trait space (Devictor et al. 2010). From two to three axes were needed to explain at least 85% of the variance (Table 2). The Gower matrix to calculate FD was estimated according to the selected PCA axes. Calculation of MPD was performed using the melodic function (de Bello et al. 2016).

Table 2. PCA loadings and the proportion of variance of each component for the Principal Component Analysis for the 5 traits measured.

	Guadarrama NP		Ordesa-Monte Perdido NP			Central Mediterranean Andes		
	PC1	PC2	PC1	PC2	PC3	PC1	PC2	PC3
Hmax	-0.17			-0.27		0.61	-0.11	-0.47
Plant Size	-0.24			-0.72	-0.67	0.52		-0.35
SLA	0.64	-0.43	-0.33	0.40	-0.40	-0.12	0.67	-0.32
LDMC	-0.70	-0.32	-0.66	-0.47	0.51	0.54		0.73
Leaf thickness		0.84	0.67	-0.18	0.37	-0.22	-0.73	-0.15
Proportion of Variance	0.52	0.34	0.43	0.33	0.13	0.45	0.33	0.17
Cumulative Proportion	0.52	0.86	0.43	0.76	0.89	0.45	0.78	0.95

We determine the phylogenetic signal in each plant trait (and the selected PCA components) to confirm phylogenetic niche conservatism in the case of finding relation between FD and PD. We tested the phylogenetic signal with the Pagel's λ using a Brownian motion model of trait evolution (Pagel 1999), using the subset of species found in each mountain region. Pagel's λ was quantified using the 'phylosig' function in the Phytools package in R.

Structural Equation Modeling

We tested a model (Fig 1.a) which underlies a complete set of causal hypotheses based on previous knowledge allowing us to study the interplay between FD, PD and

TD, and the relationships with the biotic factor and the considered abiotic determinants (elevation, potential radiation solar and the total nitrogen content in soil). Our theoretical model proposes that each of the diversity facets, FD, PD and TD, can respond to abiotic conditions and to the type and intensity of the plant to plant interactions (Fig. 1a). These relationships could be different because each component of diversity reflects different community aspects and provides information about different assembly processes. We hypothesized that FD would depend on abiotic and biotic factors because the selected traits are known for responding to these key determinants of community structure in alpine ecosystems (Dainese et al. 2015; Pescador et al. 2015). In the same way, if selected plant traits are phylogenetically conserved, PD would respond rather similarly to such environmental factors and to be structured (Cavender-Bares et al. 2004; Swenson et al. 2007). If this is not the case and the paths to both diversities are different, we could suggest that environmental determinants affecting PD are reflecting the existence of other unmeasured traits with phylogenetic signal. TD is expected to be directly influenced by FD and PD, although these relationships will depend on the degree of functional redundancy in the selected traits (FD) and in the unmeasured traits (PD) (Petchey & Gaston 2002). However, regardless of indirect effects on TD of environmental forces through FD and PD, we expect that the elevational gradient, the nitrogen in soil and the biotic component to be critical determinants structuring directly the species richness (TD). This implies that the TD can be affected by the ecological determinants both directly or indirectly through TD and PD. Finally, we considered that environmental conditions generated by the abiotic gradients could directly affect prevalence of plant interactions (considered endogenous variable) and indirectly the interplay among components of diversity through biotic interactions. Since relationships among the different environmental can have idiosyncratic effects of the mountain range

on components of diversity, the model was evaluated for each region separately, and if necessary thoroughly through with a multisample test to detect thus paths with different behaviors between mountains.

To test the theoretical model we used a Structural Equation Modelling (SEM). SEM allows to test causal links established in an initial hypothetical framework comparing the variance-covariance structure that describe the relationships between all variables taking into account the constraints imposed by the theoretical hypothesis, with the observed variance-covariance structure (for more details, see: Mitchell 1992; Iriondo et al. 2003; Maestre et al. 2005; Grace 2006). If discrepancies are small we can assume that the observed pattern is compatible with our hypotheses. The three abiotic factors represented the exogenous variables, whereas the abiotic variable and the three components of the diversity components corresponded to the endogenous variables (Fig. 1a). Standardized path estimates of path coefficients were obtained using the maximum likelihood method because is robust against certain deviations of multinormality (Shipley 2000). We used standardized coefficients to interpret scaling relationships among variables. Total nitrogen for the Ordesa-Monte Perdido NP was log-transformed to reach normality. The discrepancies between observed and expected covariance matrices was first assessed by a chi-square goodness-of-fit statistic (χ^2). In this case, P-value above 0.05 indicates between that the observed and model implied covariances are not significantly different, suggesting adequate model fit. Since this test is prone to several statistical errors especially when thee sample size is large we also used two additional measures of the goodness of fit: the comparative fit index (CFI) and the Bentler and Bonett's normed-fit index (NFI) (Iriondo et al. 2003). Before analyses and to be sure that our data sets were multinormal we calculated the variance inflation factor

(VIF) for each variable since all VIF values were < 10 (Petraitis et al. 1996). SEM were conducted using Amos v18 (SPSS, Chicago, Illinois, USA).

Figure 1. Path diagram (and structural equation model results) representing hypothesized causal relationships among the components of diversity (TD, FD and PD) and their abiotic and biotic determinants. a) Theoretical model, and models tested for b) Guadarrama NP, c) Ordesa-Monte Perdido NP and d) the central Mediterranean Andes. Positive effects, solid blue lines; negative effects, broken orange lines. Arrow widths are proportional to adjacent standardized path coefficients. Path coefficients non significantly different from zero are omitted. Goodness-of-fit statistics (χ2, GFI and NFI) and sample size (N) are provided at the upper-left corner of each diagram.
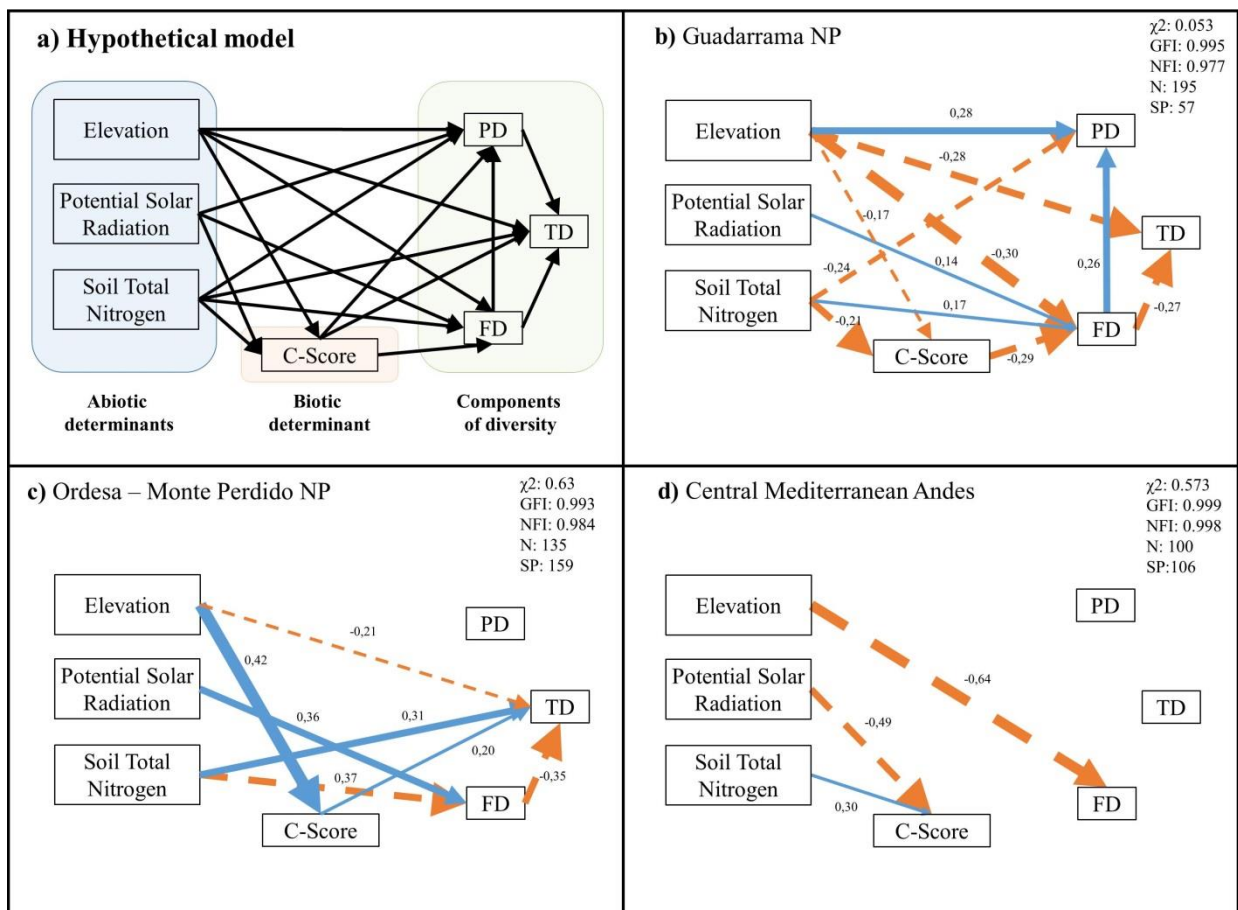
Results

We registered the presence of 57 species in Guadarrama NP (n= 195 quadrats for our SEMs), 159 species in Ordesa-Monte Perdido NP (n = 135 quadrats) and 106 species in the central Chilean Andes (in 100 quadrats). The average number of species per quadrat was of 11 species in both Mediterranean mountains (Guadarrama NP and the central Chilean Andes) being the richest mountain Ordesa-Monte Perdido NP with an average of 19 species per quadrat. The five most frequent species in Guadarrama NP (*Festuca curvifolia*, *Rumex angiocarpus, Jurinea humilis Sedum brevifolium* and *Jasione crispa* subsp. *centralis*) occurred at least in a 67% of the quadrats, whereas in Ordesa-Monte Perdido NP (*Thymus serpyllum, Koeleria vallesiana, Galium pyrenaicum, Festuca gautieri* subsp. *scoparia* and *Helictotrichon sedenense*) and in the central Chilean Andes (*Poa denudate, Trisetum presley, Hordeum comosum, Phacelia secunda and Bromus setifolius)* these species were registered in a 36% and 32% of quadrats respectively. The central Chilean Andes was characterized by a strikingly nutrient poor soil in total nitrogen (0.6 mg / g^{-1}) in comparison to the others mountain ranges (>3 mg / g^{-1}, see Table 1).

To assess whether patterns of covariation among the components of diversity (TD, FD and PD) and their abiotic and biotic determinants were consistent with predictions of our theoretical causal model in the three mountain ranges, we built three models (one for each region). All of them were significant but contrarily to our expectations they were markedly different so we did not conduct a multisample analysis. The model for Guadarrama NP provided a good fit to observed data because it had a non-significant $\chi 2$ ($\chi 2$=7.74, DF=1, P=0.053) and the values of NFI and GFI were higher than 0.90 (Fig 1b). Soil nitrogen and potential solar radiation had a positive

effect on FD while the effect of elevation and the c-score was negative. However, in spite of positive relationship between FD and PD suggesting phylogenetic conservatism, PD was influenced by soil nitrogen and elevation in a way contrary to FD (Fig. 1b). TD was negatively affected by elevation whereas the interplay between FD and TD was also negative.

The model for Ordesa-Monte Perdido NP received high statistical support, as suggested by non-significant $\chi2$ values ($\chi2=3.45$, DF=1, p=0.063) and by values of NFI and GFI higher than 0.9, indicating that field data adjust the theoretical model (Fig. 1c). In contrast to the results for the Guadarrama's model, in this case the strength of the model was mainly due to the strong relationship between the environmental predictors and TD (Fig. 1c). TD was positively affected by soil nitrogen and c-score while elevation had a negative effect on TD. FD was positively influenced by solar radiation and negatively by soil nitrogen. The negative relationship between FD and TD found in the Guadarrama model was again observed here (Ordesa-Monte Perdido NP model). However, any significant relationship between other variables and PD were significant (Fig. 1c).

Finally, the model for the central Chilean Andes was also satisfactorily fitted as indicated by the non-significant $\chi2$ values ($\chi2=3.18$, DF=1, p=0.573) and the NFI and GFI values, which were again far above 0.90 (Fig. 1d). However, in this case an exclusive significant influence was detected between elevation and FD in spite of the strong causal relationships between soil nitrogen° and potential solar radiation with the surrogate of biotic interactions (c-score) (Fig. 1d).

We found significant phylogenetic signal in all traits for the plants from the central Mediterranean Andes. In Guadarrama NP and Ordesa-Monte Perdido NP,

significant phylogenetic signal was found in all plant traits except specific leaf area (SLA; Table 3). For each of the PCA axes obtained from the plant functional traits only in Guadarrama NP were significate and close to one, indicating phylogenetic signal in the data (Table 3).

Table 3. Phylogenetic signal in 5 functional traits and in the according to Pagel's λ metric using the subsets of species found in each mountain region. The significance is shown as *, p<0.01 and ***, p<0.001.

	Guadarrama NP		Ordesa-Monte Perdido NP		Central Mediterranean Andes	
Hmax	0.86	***	0.37	***	0.24	***
Plant Size	0.99	***	0.69	***	0.84	***
SLA	0.31		0.00		0.56	*
LDMC	0.87	***	0.60	***	0.66	***
Leaf thickness	0.67	*	0.94	***	0.59	*
PC1	0.78	***	0.88	***	0.76	****
PC2	0.69	*	0.51	***	0.49	
PC3			0.14		0.04	

Discussion

To progress toward a unified framework of coexistence of species we tested a working model across different mountain ranges with different evolutionary history, disturbance regime, and climatic conditions for evaluating the generality of the responses of the plant community structure to the local environmental determinants. The results obtained confirmed that our model adequately describe the observed data in the three mountain ranges (Fig. 1b-d), suggesting empirical evidence for a direct relationship among the abiotic and biotic environments, and the underlying community structure inferred from the patterns of the different components of diversity (TD, FD and PD). Although numerous studies have revealed abiotic determinants shape diversity in any of its facets (Bernard-Verdier et al. 2013; Oliver et al. 2013; Dainese et al. 2015), our study represents a first attempt to define how the abiotic constrictions together with the role played by plant-plant interactions, which are modulated in turn by the same constrictions, determine the interplay among the TD, FD and PD in alpine communities. Our approach also reveals that under certain circumstances the indirect relationships with the ecological determinants may be different to those reflecting direct links. Worth also to note that our hypothetical model is compatible with the three data sets although the causal links varies between mountain suggesting important idiosyncratic differences.

We found that FD was strongly influenced by various environmental variables, being the unique community component of diversity that responded to environment in the three mountain ranges (Fig. 1b-d) supporting the extended idea that the assembly process at fine spatial scales is catalyzed by the functional configuration of the species involved (Keddy 1992; Weiher & Keddy 1995). Moreover, FD influenced directly TD in the two mountain ranges from Spain, and it also influenced PD in Guadarrama NP,

reinforcing the importance of the role of the FD in the community assembly. Other studies, however, have shown different signs in the relationships of FD and the other components of diversity. Pillar & Duarte (2010) found that phylogenetic structure is the responsible for structuring FD following the temporal perspective in which the evolutive/historical relationships go first in the assembly process, whereas Pavoine (2013) among others authors, have proposed that TD influence the other components of diversity (Flynn et al. 2011; Pavoine et al. 2013). Our results are congruent with our hypothesis that the FD should be the main facet of diversity that responds in first instance to ecological sorting pressures and which facilitates detecting the imprints of the assembly processes in the communities (Shipley et al. 2016), as long as the appropriate traits are measured. Nevertheless, in Ordesa – Monte Perdido NP the TD was the component of diversity which was the most affected by the environmental determinants and it was also restricted by elevation in Guadarrama NP suggesting species richness captures other important aspects of diversity and assembly. Thus, species and functional traits could provide different and complementary information, and combining them, our potential to reveal the processes that structure biological communities patently increase (Díaz & Cabido 2001; Mouchet et al. 2010; Bernard-Verdier et al. 2013). Additionally, we found few significant relationships in which PD was involved. In accordance with previous studies, this suggests that PD is a poor indicator of current assembly processes (Pavoine et al. 2013; Gerhold et al. 2015).

In spite of the good fit of the observational data as a whole to the constraints imposed by our model, we found a high degree of idiosyncrasy with evident differences between mountains. Indeed, we found that some relationships even shifted from positive to negative between mountain ranges. This suggests that some relationships are strongly context-dependent, making it difficult to draw general conclusions so we

should yield specific conclusions of each particular site. First, elevation was negatively and positively relate to the c-score metric at Guadarrama NP and Ordesa – Monte Perdido NP respectively. Additionally, soil total nitrogen affected positively the FD at Guadarrama NP whereas at Ordesa – Monte Perdido NP total nitrogen content influenced negatively FD (Fig 1b). In the case of the co- occurrence patterns, we expected an interspecific aggregation with increasing environmental severity (elevation) in all mountain ranges due to the prevalence of facilitation (Choler et al. 2001; Callaway et al. 2002). However, the role of facilitation decreased with increasing elevation in Ordesa - Monte Perdido NP. We speculated that in this Eurosiberian mountain without summer drought the environment conditions were particularly harsh at the top collapsing the facilitative interactions, as suggested by Soliveres et al. (2012) in extremely arid environments. It is also worth to comment that other mechanisms, such as an increasing heterogeneity in site conditions with elevation cannot be ruled out as an additional explanation for this segregation of species (Dullinger et al. 2007). On the other hand, the large discrepancies around the relationship between total nitrogen and FD correspond with those found in the literature (Pakeman et al. 2011; Mason et al. 2012; Spasojevic & Suding 2012). It is well known that plant community diversity respond to soil fertility and their properties in an unimodal way (Grime 2006) so, the sign of the underlying relationship may depends on represent segment of the hump in which we were working. Therefore, the relationship between FD and total nitrogen may represent the ascending and descending sides at Guadarrama NP and at Ordesa- Monte Perdido NP respectively. Taken all together it can be suggested that the dominant assembly mechanisms could vary from an environmental filtering in the Mediterranean region (Grime 1973) to various competition-related mechanisms in the Eurosiberian region (Grime 1977; Weiher et al. 1998). Even these differences in nitrogen can be

mediated through other drivers such as cattle grazing (Afzal & Adams 1992; Liu et al. 2016) that alters the concentration of nitrogen affecting the functional diversity and structure of the communities (de Bello et al. 2006). In any case, grazing in our mountains is absent or simply residual which suggest herbivory by domestic cattle is irrelevant.

Despite our results shown a high variability among regions, we found constant patterns that indicate that some processes within the same ecosystem could be generalized. The main consistent result is that increasing elevation significantly affects the functional and taxonomic community structure, which is always reduced at the upper elevational limit. This result is one of the most commonly reported patterns for alpine environments (Rahbek 1995; de Bello et al. 2013; Read et al. 2014; Cuesta et al. 2017). The severity of the environmental conditions usually increases with elevation, which reduce the trait range values and diversity observed within communities, limiting the number of the plant species that can establish and survive in such a stressful environments (Weiher & Keddy 1995; Cornwell et al. 2006). It is noteworthy that in Guadarrama NP the increase in elevation generated an increase in PD opposite to the decline in FD in spite of PD was positively correlated with FD, which was consistent with the strong phylogenetic signal found in the considered functional traits (Table 3). Although an decrease in PD have been generally described in the literature (Bryant et al. 2008; Graham et al. 2009; Machac et al. 2011) specially in plants (Li et al. 2014; Xu et al. 2017), discrepancies between the functional and phylogenetic structures have been also reported in an high-elevation grasslands in the European Alps (Dainese et al. 2015). An potential explanation for the this striking result is the hypothesis of Valiente-Banuet & Verdú (2007), who proposes that an increase the PD can be driven by facilitation whose importance increased when environment conditions became more stressful. This

increase in the strength of facilitation was also supported by the fact that elevation leads low levels of the c-score. This can be interpreted as the prevalence in positive interactions among plants (Dullinger et al. 2007; Schöb et al. 2013).

Additionally, we found a negative relationship between FD and TD which was consistent at the Guadarrama NP and Ordesa-Monte Perdido NP (Fig. 1 b-c). This relationship suggest the existence of ecological redundancy in the richer assemblages (Naeem 1998; Loreau 2004). These findings contrast with the intuitive hypothesis that higher FD require a higher species richness (Petchey & Gaston 2002). Similar to our results, de Bello et al. (2009) found in alpine pastures in the Catalan Pre-Pyrenees an increase in functional redundancy associated with an increase in species diversity. Our results indicate that the volume of functional plant trait space is occupied by just few species in all communities and new species entering with increasing richness are not different from those already present (Díaz & Cabido 2001). This strong niche overlap among species can be interpreted as the result of the existence of a strong abiotic filtering on the whole alpine community related to harsh environmental conditions alpine plants must endure. Besides, particularly interesting was this consistency of the relationship across regions sharing regional species pool and similar evolutionary histories. It is important to note that the FD decreases when a redundant species enter in the community if a metric based on average pairwise dissimilarity (such as the MPD) is considered.

The structural equation modelling approach adopted in this study provides insight into the potential underlying mechanisms that shape community structure in alpine plant communities. This study adds to empirical evidence that a balance between competition and facilitation produced by changes in environmental conditions together

with an strong environmental filtering are common in alpine environments. However, caution must be posed in extrapolating such local processes to other species pools due to idiosyncratic effects across environmentally similar ecosystems. Our results highlight the importance of considering the different components of diversity (TD, FD and PD). Although the traits are expected to respond directly to the environmental drivers, our results encourage using the taxonomic (almost forgotten in later years) and the phylogenetic information, in spite of species and phylogeny are unable to capture all aspects of functional community structure (Mouchet et al. 2010). However, they capture different and complementary information about community assemblage processes. Disentangling the interplay among these facets can reveal critical processes such as conservatism or redundancy.

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Discusión general

Esta Tesis aborda la búsqueda de las reglas ecológicas de ensamblaje en comunidades naturales de plantas de alta montaña y la identificación de los principales mecanismos responsables que estructuran la diversidad, prestando especial atención a algunas de las limitaciones que restringen el progreso hacia un margo global para la teoría de coexistencia. Avanzar hacia un marco global que nos permita entender cómo se produce el ensamblaje de las comunidades y que explique qué determinantes conducen la convivencia de las especies constituye una de las prioridades de la investigación en ecología, aunque si bien es cierto este marco permanece todavía en su infancia (Swenson 2011). Hasta ahora, existe un amplio consenso de que el ensamblaje de las comunidades está mediado por procesos puramente estocásticos o azarosos, junto con los procesos deterministas los cuales se rigen por reglas que subyacen a las constricciones que imponen las condiciones ambientales y las interacciones del medio abiótico en las comunidades (Wilson 1999; Chase et al. 2011; Götzenberger et al. 2012; HilleRisLambers et al. 2012; Vellend et al. 2014; Escudero & Valladares 2016).

A pesar de tener un marco definido continúan existiendo numerosas discrepancias a la hora de encontrar las reglas de ensamblaje, incluso cuando se buscan en los mismos ecosistemas y regiones. Algunos de estos elementos que limitan el avance hacia un marco unificado tienen que ver con aspectos que van desde aquellos metodológicos que se producen a la hora de fijar la escala de estudio (McGill 2010; Chase 2014; Münkemüller et al. 2014; Harmon & Harrison 2015), hasta aquellos que están relacionados con el uso de metodologías analíticas desfasadas y que no son capaces de discernir entre mecanismos causantes de los patrones. Así la discusión general de la presente tesis está por tanto centrada en dos aspectos principales: (1)

cuáles son las reglas ecológicas de ensamblaje que prevalecen en la configuración de las comunidades de plantas de alta montaña; y (2) en qué medida se han salvado las limitaciones de las que adolece el marco actual y que permiten un avance en la teoría de la coexistencia de especies.

Aunque sabemos que los procesos subyacentes al ensamblaje pueden actuar a diferentes escalas espaciales, actualmente no existe un consenso que determine la escalo-dependencia de los patrones de diversidad en las comunidades a los procesos ecológicos subyacentes (Leibold et al. 2004; Burton et al. 2011). Así, no conocemos el tamaño ideal de la escala espacial que se debería usar para detectar los distintos mecanismos de ensamblaje (Magurran 2004). Conscientes de esta limitación, propusimos una aproximación multiescalar desde el punto de vista espacial definiendo tres escalas de manera jerarquizada y se estudió el efecto de varios factores los cuales se esperan que actúen a distinta escala en la estructura de las comunidades. Así esperamos que la altitud afecte a las diversidad de especies a una escala regional, mientras que otros componentes más conspicuos de heterogeneidad ambiental como la insolación o la fertilidad del suelo, esperamos que lo hagan a escala de localidad y microhábitat respectivamente, siendo las interacciones bióticas las actuarían a escala de parche, donde se producen los contactos entre especies (Leibold et al. 2004). Cuando se observó el efecto de estos factores en la diversidad taxonómica de los Andes chilenos, tanto a nivel alfa como beta, pudimos corroborar la importancia de considerar el enfoque multiescalar para dilucidar los mecanismos que estructuran la diversidad de plantas de alta montaña. Encontramos que el efecto de algunos factores solo fue identificable a escalas específicas. Por ejemplo, la altitud influyó en la riqueza, la diversidad beta y la productividad de la planta a la escala mayor, mientras que el componente biótico solo tuvo efecto en las escalas más pequeñas (Capitulo 1). Estos resultados se ajustaron a lo

esperable, sin embargo, cuando la influencia de la fertilidad del suelo fue estudiada sobre la diversidad taxonómica, este efecto fue constante a lo largo de las tres escalas. Esto puede deberse a que la heterogeneidad ambiental asociada a los nutrientes del suelo es muy alta y se presenta a un grano muy fino, cuyos efectos netos se proyectan a escalas grandes de la misma manera (Reynolds et al. 2007). Probablemente si incrementásemos el grano progresivamente, llegaría un momento que dejaríamos de encontrar el efecto debido a la hominización que sufriría la variable.

Por otro lado, resulta muy sorpréndete que cuando la diversidad funcional (FD) y la diversidad filogenética (PD) de las comunidades de plantas fueron estudiadas en los Andes mediterráneos chilenos (Capítulo 2) nuestros resultados indicaron que la intensidad de los procesos de ensamblaje permanecieron constantes a lo largo de las escalas espaciales (Chalmandrier et al. 2017). Varios factores podrían explicar esta discrepancia. Por un lado, se estudiaron diferentes aspectos de la diversidad, y si bien es cierto, cada aspecto puede responder a los factores ambientales tanto bióticos como abióticos en distinta dirección, ya que representan información muy diferente (Devictor et al. 2010; Pavoine & Bonsall 2011). En este caso, la respuesta de la FD y la PD puede ser más sensible que la diversidad taxonómica (TD) a los cambios bruscos en las condiciones abióticas ambientales que generan la interacción entre el gradiente de insolación y la altitud. Por otro lado, hay que sumar que la aproximación metodológica que se usó para analizar la estructura de la DF y la DP no fue la misma que la que se usó para analizar la DT. En el segundo capítulo, las diversidades (FD y PD) fueron enfrentadas a las diversidades esperadas bajo un modelo nulo concreto, con lo cual, se modeliza una propiedad emergente que "poco" tiene que ver con las características brutas de la comunidad.

El modelo nulo usado en el capítulo 2 fue un modelo que aleatoriza la matriz de datos observada en toda la zona de estudio manteniendo fija la riqueza de especies observada en las comunidades y la tasa de ocupación de las especies en todo el sistema de estudio (Gotelli & Entsminger 2003). La elección de este modelo nulo tiene sentido ecológico, ya que el número de especies de una comunidad está relacionado con el pool regional, las limitaciones a la dispersión, la capacidad de carga de territorio y la competencia. Por el otro lado, la tasa de ocupación de las especies es una estima de la probabilidad de ocurrencia de la especie seleccionada. Esto indica que este modelo nulo es muy restrictivo por lo que encontrar patrones significaría que algún mecanismo está generando los patrones encontrados.

En el capítulo 3 para avanzar en la búsqueda de mecanismos concretos usamos un enfoque novedoso para incorporar determinantes abióticos y bióticos (es decir, reglas de ensamblaje ecológico) en modelos nulos para revelar el papel desempeñado por dos procesos deterministas críticos, condiciones abióticas e interacciones bióticas en la ensamblaje de las comunidades. Las comparaciones entre la estructura funcional de los conjuntos observados y la estructura funcional esperada bajo el efecto de reglas de ensamblaje de mecanismos abióticos, bióticos o ambos, nos permiten inferir si estas dos fuerzas ecológicas críticas individual o simultáneamente determinan el ensamblaje de las comunidades y, de ser así, su prevalencia relativa a lo largo de los gradientes ambientales. Aunque todos nuestros tres modelos nulos realistas son capaces de reproducir la estructura funcional para los rasgos múltiples, pero también para todos los rasgos de plantas individuales considerados, su rendimiento varió a lo largo de los gradientes ambientales considerados.

En general, nuestros resultados mostraron que el número de cuadrantes donde el porcentaje de FD era más bajo de lo esperado era casi inexistente para todos los modelos nulos considerados y rasgos que indicaban que los algoritmos de modelo nulo describían con precisión el ensamblaje funcional de la comunidad (Tabla 1). Una consideración preliminar del funcionamiento de este pastizal de alta montaña rico en especies de los Pirineos Centrales sugeriría que las reglas abióticas y bióticas serían igualmente importantes en la estructuración de la configuración funcional de las comunidades. Sin embargo, al evaluar el rendimiento de los modelos nulos, encontramos diferencias importantes. Por ejemplo, mientras que las frecuencias de aparición de especies generadas bajo los modelos bióticos y mixtos abióticos-bióticos nulos fueron muy similares a las observadas en la matriz comunitaria, las generadas bajo los modelos abióticos nulos fueron bastante diferentes (Figura 1). En este último caso, encontramos un grupo de especies, que corresponde a las más frecuentes, cuyas frecuencias de ocurrencia tienden a ser proporcionales a las frecuencias observadas, mientras que las especies raras (es decir, especies presentes en menos del 20% de cuadrantes) aparecieron en el null conjuntos con la frecuencia que tendrían en un conjunto aleatorio no ponderado, que es por mucho más grande que el observado.

Además, el modelo abiótico nulo también fue el peor modelo nulo que reproduce la composición de ensamblajes (Apéndice 1), sugiriendo que los procesos abióticos en sí mismos no son capaces de explicar completamente los patrones observados, y por lo tanto, otros procesos tales como interacciones bióticas son necesarios para reproducir mejor la configuración funcional de la comunidad (Cornwell y Ackerly 2009, de Bello et al., 2012). De hecho, al analizar las relaciones entre los SES de FD para cada rasgo único y multi-rasgo a lo largo de gradientes ambientales conspicuos, detectamos relaciones significativas con los gradientes ambientales con el modelo abiótico nulo

(Fig. 2). Específicamente, los FD más grandes en valores absolutos se encontraron en ambos bordes de los gradientes de radiación elevacional y solar. Este resultado sugiere que las interacciones bióticas pueden ser mucho más importantes en estas partes de los gradientes (Michalet et al., 2006) que son mucho más estresantes.

Vale la pena señalar que se encontró un aumento en la radiación solar potencial derivado de la divergencia funcional a la convergencia en la altura de la planta y la masa de la semilla. La radiación solar es un proxy del aporte de energía, que puede afectar negativamente el rendimiento de las especies de plantas alpinas en términos de equilibrio hídrico y evapotranspiración (Mooney et al., 1965; Ritchie, 1998). Sin embargo, en los sistemas alpinos como los Pirineos centrales como en otras montañas templadas donde las tormentas de verano son frecuentes, la radiación solar parece ejercer un efecto positivo al alargar la estación de crecimiento efectiva a través del deshielo temprano (Körner 2003). Estudios previos en sistemas similares también han detectado una tendencia a la convergencia de la masa de semilla con el aumento de la radiación solar (de Bello et al., 2013) e incluso la convergencia en la altura de la planta en las primeras zonas de fusión (Venn et al., 2011). En nuestro caso, los patrones de convergencia en altura de planta y masa de semilla no deberían estar mediados por condiciones abióticas porque las comunidades nulas se generaron con un modelo mecanístico con parámetros que especifican procesos abióticos (Chalmandrier et al., 2013; Botta-Dukát & Czúcz 2016) Nuestros resultados respaldan la idea de que en condiciones más relativamente benignas, los patrones de convergencia de rasgos pueden deberse a procesos competitivos, que clasifican las especies con diferentes capacidades competitivas (es decir, excluyen menos especies tolerantes al estrés) (Mayfield & Levine 2010). Cabe destacar que los pastizales pertenecientes a la alianza Festucion scopariae tienen preferencia por los sitios con mayor radiación solar (Alonso 2005),

mientras que, en otras localidades menos aisladas, es probable que se evite la capacidad competitiva de las especies que dominan la comunidad. para otras plantas, funcionalmente diferentes que pueden ingresar a la comunidad.

La divergencia funcional de la altura máxima de la planta, el grosor de la hoja y la variabilidad multi-rasgo aumentaron con la elevación (Fig. 2). Los mecanismos que inducen una mayor dispersión funcional están asociados en la literatura a dos procesos opuestos: la competencia (MacArthur & Levins 1967) o la facilitación (Soliveres et al., 2012; Gross et al., 2013). La "hipótesis del gradiente de estrés" sugiere que la facilitación prevalecerá sobre la competencia a medida que aumenta el estrés ambiental (Michalet et al. 2006) y, por lo tanto, se espera que los procesos de facilitación aumenten debido a condiciones ambientales extremas (Callaway et al., 2002; Chalmandrier et al. 2017). Además, encontramos el mismo efecto de elevación en la altura máxima de planta FD usando el modelo nulo biótico (Fig. 3). Este resultado sugiere que la variación de la convergencia funcional a la divergencia funcional a lo largo del gradiente altitudinal no solo debe ser causada por mecanismos bióticos, sino también por factores abióticos. Sin embargo, hay muchas posibles interpretaciones de este resultado porque hay muchos posibles factores geofísicos relacionados con los gradientes altitudinales, como se resume en Körner (2007). Otra posible explicación para este patrón puede implicar los efectos de los regímenes de perturbación en la variación del rasgo, en particular el pastoreo de ganado cuya intensidad aumenta a bajas elevaciones. Por lo tanto, las especies que carecen de rasgos para persistir bajo condiciones de pastoreo serían eliminadas de la comunidad (Díaz y otros 2001, de Bello et al., 2006; Ding et al., 2012), disminuyendo la diversidad funcional. De hecho, , las plantas hemicriptofitas dominantes en pastizales intensivos comparten tamaños de plantas similares.

En las últimas dos décadas, los ecologistas se han interesado cada vez más en encontrar formas de revelar los procesos que impulsan el ensamblaje comunitario desde la perspectiva de la ecología funcional, pero no se ha llegado a un consenso sobre cuál es el protocolo más apropiado para generar comunidades nulas (Gotelli Y Graves 1996). Proporcionamos algunas ideas sobre los nuevos avances teóricos y metodológicos en el análisis de modelos nulos para la evaluación de la importancia relativa de los procesos y mecanismos subyacentes al ensamblaje de la comunidad. Nuestro enfoque reveló la importancia de utilizar modelos nulos apropiados con una clara conexión con los procesos impulsados por la ecología para detectar con éxito los mecanismos subyacentes que dan forma a la estructura funcional de las comunidades de plantas (de Bello 2012).

La generación de ensamblajes nulos bajo la acción de una regla de ensamblaje ecológico particular permite comparar patrones observados y esperados y decidir si las comunidades observadas son compatibles con dicha regla ecológica. Específicamente, nuestros resultados destacan el potencial de los modelos nulos con limitaciones ambientales para evaluar el efecto de las interacciones bióticas, como la facilitación o la competencia. Por lo tanto, nuestros resultados indican que las interacciones bióticas son un factor crítico del ensamblaje comunitario en los ecosistemas alpinos mientras que la clasificación de especies debido a los procesos ambientales parece jugar un papel relativamente más débil al menos en resoluciones espaciales finas como las consideradas en este estudio.

En este contexto, quisiéramos destacar dos advertencias importantes para estudios futuros: (1) es importante enfatizar la utilidad de los modelos nulos para comparar patrones, pero se debe prestar atención para inferir mecanismos de ensamblaje

comunitario porque los diferentes procesos podrían dar los mismos resultados (Kraft et al. 2015) (2) Fijamos la riqueza de especies en cada sitio en nuestros modelos nulos, suponiendo que la capacidad de carga de cada sitio es diferente en función de las condiciones ecológicas locales, como la fertilidad del suelo y el estrés abiótico. Por lo tanto, la detección de procesos bióticos podría difuminarse ya que la riqueza de especies también es el resultado de interacciones competitivas. Esperamos inspirar más estudios que contribuyan a construir un marco metodológico unificador para el análisis de ecología funcional.

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Conclusiones

De los resultados obtenidos en esta tesis doctoral se pueden extraer las siguientes conclusiones generales:

- La estructura de las comunidades de plantas alpinas subyace a las reglas ecológicas de ensamblaje, tanto bióticas y como abióticas. Un complejo equilibrio entre competencia y facilitación producido en respuesta a la variabilidad en las condiciones ambientales, junto con el filtrado ambiental que producen las bajas temperaturas de alta montaña, son los principales mecanismos que determinan la estructura de las comunidades de plantas de alta montaña en nuestra zona de estudio.

- Los mecanismos responsables de causar y mantener los patrones de diversidad taxonómica pueden diferir en regiones sometidas a distinto régimen climático en los Andes Chilenos. La respuesta unimodal de la riqueza al gradiente altitudinal parece estar influenciado por la sequía estival la cual se intensifica a baja altitud, mientras que en los Andes Sub-antárticos donde la sequía es despreciable, parece que la facilitación que producen las especies nodriza sobre otras especies puede subir ligeramente el número de especies en las comunidades a cotas intermedias donde abundan estas especies y el estrés no llega a ser extremadamente fuerte.

- El efecto de los determinantes bióticos y abióticos en la diversidad taxonómica ve incrementada su intensidad a escalas específicas. La respuesta de la comunidad a la altitud prácticamente fue detectable a la escala de parcela, mientras que el efecto de las interacciones bióticas solo fue patente a escalas pequeñas donde las plantas interactúan.

- El estrés en las montañas mediterráneas chilenas es intenso en ambos extremos del gradiente altitudinal debido a la existencia de gradientes opuestos como son el de temperatura y humedad. Además, la radiación solar puede atenuar o

exacerbar la dureza ambiental asociada al gradiente altitudinal. En consecuencia, la interacción entre estos factores produce divergencia funcional y filogenética como resultado de las interacciones facilitadoras donde las condiciones son más estresantes. Por el contrario, cuando las condiciones son más suaves, el dominio de unas pocas especies que son más competitivas podría conducir a patrones de convergencia funcional.

- La diversidad filogenética proporciona información relevante cuando los rasgos seleccionados no tienen señal filogenética e incluso responden en el mismo sentido a los determinantes ambientales.

- Al menos en resoluciones espaciales pequeñas, las interacciones bióticas son un factor crítico del ensamblaje de las comunidades en los ecosistemas alpinos del centro de Pirineos. El uso de modelos nulos que representan la acción de reglas abióticas ensamblando las comunidades nulas a partir de constricciones ambientales, presentan un gran potencial para evaluar el efecto de las interacciones bióticas, como la facilitación o la competencia.

- La evaluación de la dispersión funcional a lo largo de múltiples gradientes de estrés ayuda a interpretar los patrones encontrados, dado que diferentes mecanismos pueden producir los mismos patrones (p.e. la facilitación y la competencia pueden generar divergencia funcional). Además, considerar interacciones entre gradientes, ya sean aditivas o sinérgicas, pueden revelar nuevas perspectivas para los procesos de ensamblaje de las comunidades.

- Se debe tener precaución al extrapolar procesos de ensamblaje que ocurren en sistemas alpinos particulares a otros ambientalmente similares debido alto grado de idiosincrasia que hay en las relaciones entre el entorno y la estructura de la comunidad. Si bien es cierto, hay relaciones tan potentes que pueden ser generalizadas a lo largo del planeta como es la disminución de la riqueza de especies con la altitud, al menos en el tramo final del gradiente donde el número de especies que son capaces de sobrevivir a tales condiciones extremas caen bruscamente.