UNIVERSIDADE DE SÃO PAULO
INSTITUTO DE BIOCIÊNCIAS
Programa de Pós-Graduação em Ecologia

Redes Tróficas do Pleistoceno: Estrutura e Fragilidade

Pleistocene Trophic Networks: Structure and Fragility

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Tese apresentada ao Instituto de Biociências da Universidade de São Paulo para obtenção de título de Doutor em Ciências na área de Ecologia.

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"All knowledge is good. It is impossible
to say any fragment of knowledge,
however insignificant or remote
from one's ordinary pursuits, may
not some day be turned to account."

Thomas Henry Huxley

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RESUMO

A extinção de grandes mamíferos terrestres no final do Pleistoceno (entre 50 e 11 mil anos atrás) é um dos temas mais debatidos em ecologia. A maioria dos estudos sobre as causas das extinções do Pleistoceno tem como foco o papel de fatores externos como mudanças climáticas e a chegada do homem. Entretanto, a forma como uma comunidade ecológica responde a perturbações depende de suas propriedades, como o número e composição de espécies e a forma como essas espécies interagem. O objetivo final dos estudos reunidos nessa tese foi entender como estavam organizadas as interações ecológicas entre os mamíferos do Pleistoceno e o possível papel dessas interações no episódio de extinção da megafauna. Em primeiro lugar adaptei modelos de teias tróficas para reproduzir redes formadas por diferentes tipos de interações entre consumidores e recursos. Em seguida, utilizei esses modelos para reconstruir redes de interação entre predadores e presas da megafauna do Pleistoceno e examinei as propriedades estruturais e dinâmicas dessas redes. Por fim, investiguei uma das possíveis consequências da extinção da megafauna: a perda de serviços de dispersão de sementes. Os resultados aqui apresentados mostram que (i) diferentes tipos de redes de interação entre consumidores e recursos compartilham características estruturais e podem ser reproduzidas por modelos de teias tróficas; (ii) redes de interação entre grandes mamíferos do Pleistoceno estavam, provavelmente, estruturadas de forma similar aos sistemas atuais na África. Entretanto, as comunidades do Pleistoceno seriam especialmente vulneráveis às mudanças estruturais e na dinâmica causadas pela chegada de um predador como o homem; (iii) entre as consequências da extinção do Pleistoceno está a reorganização de outros tipos de rede de interação como as redes de dispersão de sementes. Em conjunto os resultados apresentados aqui enfatizam a importância de considerarmos o possível papel das interações ecológicas em modular os efeitos de perturbações ao estudarmos eventos de extinção.

ABSTRACT

The extinction of large terrestrial mammals during the late Pleistocene (between 50 and 11 kyrs ago) is one of the most debated topics in ecology. Most studies on the causes of Pleistocene extinctions focus on the role of external factors such as climate changes and the arrival of humans. Nevertheless, the way an ecological community responds to perturbations depends on its properties, such as its number of species, species composition and the way these species interact. This thesis encloses studies with the final objective of understanding how ecological interactions between Pleistocene large mammals were organized and the potential role of such interactions in the Pleistocene extinction episode. First, I adapted food-web models to reproduce networks depicting different types of ecological interactions between consumers and resources. Then, I used these models to reconstruct predator-prey interaction networks between Pleistocene large mammals and examined the structural and dynamic properties of these systems. Finally, as an overview of the ecological impacts of Pleistocene extinctions, I discuss one of the possible consequences of the demise of Pleistocene large mammals: the loss of seed-dispersal services. The results presented here show that (i) different types of interaction networks between consumers and resources share structural properties and can be reproduced by food-web models; (ii) interactions between Pleistocene large mammals were most likely structured in a similar way to modern large-mammals assemblages in Africa, but the former were especially vulnerable to the changes in structure and dynamics caused by a newly arriving predator such as humans; (iii) among the consequences of Pleistocene extinctions is the reconfiguration of other types of interaction networks such as seed-dispersal networks. Taken together these findings emphasize how important it is to consider the role of ecological interactions in modulating the effects of perturbations when studying extinctions events.

INTRODUÇÃO

Com exceção do continente africano, a maior parte dos mamíferos de grande porte se extinguiu antes do limite entre o fim do Pleistoceno e início do Holoceno, há aproximadamente 11,5 mil anos (Martin & Klein 1984; Koch & Barnosky 2006). O número de espécies extintas foi particularmente grande nas Américas e na Austrália, onde se estima que entre 70 e 90% dos gêneros de mamíferos classificados como megafauna (animais com mais de 44kg) foram extintos (Koch *et al*. 2006). O fenômeno destaca-se não somente pela sua magnitude, uma vez que o número de espécies extintas foi sem precedentes no Cenozóico (Alroy 1999), mas por sua seletividade em relação ao tamanho corpóreo (Koch *et al*. 2006). Ainda que espécies menores também tenham sido extintas (Brook & Bowman 2004), a extinção foi total para os mamíferos com mais de 320 kg na América do Sul e mais de 1000 kg na América do Norte (Owen-Smith 1987).

Em geral, as hipóteses propostas para explicar a extinção da megafauna do Pleistoceno são baseadas nos efeitos de fatores externos, como mudanças climáticas e a colonização dos continentes pelo homem (Barnosky *et al*. 2004). As hipóteses que sugerem a influência de mudanças climáticas como principal fator responsável pela extinção da megafauna do Pleistoceno baseiam-se no fato de o período estimado para as extinções coincidir com o período de transição entre a última era glacial e a era inter-glacial atual (Koch *et al*. 2006). As mudanças climáticas nesse período teriam causado mudanças na vegetação, finalmente levando à fragmentação e redução de habitat e disponibilidade de recursos (Barnosky 1986; Ficarelli *et al*. 2003). Essas mudanças no habitat teriam reduzido e isolado populações naturais, tendo um efeito profundo sobre as populações de grandes mamíferos, que possuem baixa taxa reprodutiva e, portanto, levam mais tempo para se recuperar (Johnson 2002). O ponto mais frágil dessas hipóteses é que estudos paleoclimáticos sugerem que essa transição não foi mais abrupta que outros períodos transitórios que não são caracterizados por grandes extinções (Barnosky *et al*. 2004, Robinson *et al*. 2005) e pelos quais os grandes mamíferos hoje extintos teriam sobrevivido (Koch *et al*. 2006).

Um segundo conjunto de hipóteses baseia-se na sincronia, em diferentes continentes, entre as extinções e a colonização pelo homem. A modificação do habitat causada pelo homem, a sobre-caça, a introdução de espécies invasoras, ou doenças letais que teriam o homem como hospedeiro, foram propostos como possíveis impactos antrópicos responsáveis pela extinção da megafauna (Martin 1973; Edwards & Macdonald 1991; Koch *et al*. 2006). Estudos teóricos que modelam as extinções considerando efeitos antrópicos sugerem que, mesmo em baixas densidades, humanos podem ter tido um papel importante no colapso das comunidades do Pleistoceno (Alroy 2001; Brook and Bowman 2004; Zuo *et al*. 2013). Críticas a hipóteses sobre o papel do homem nas extinções do Pleistoceno enfatizam o baixo número de evidências empíricas, especialmente indícios arqueológicos da interação entre o homem e as espécies atualmente extintas (Koch & Barnosky 2006, Hubbe *et al*. 2013; mas veja Surovell & Waguespack 2008). Além disso, a sincronia entre as extinções e a colonização dos continentes pelo homem tem sido contestada (Lima-Ribeiro *et al*. 2013). Atualmente, sugere-se que uma combinação entre atividades humanas e mudanças climáticas explicaria as extinções: o homem teria contribuído para a extinção da megafauna em vários locais e as mudanças climáticas teriam exacerbado esses efeitos em escalas espaciais maiores (Koch *et al*. 2006; Prescott *et al*. 2012).

Todavia, grandes eventos de extinção tem dois componentes importantes: a perturbação que desencadeou o fenômeno, como, por exemplo, mudanças climáticas ou atividade humana, e as características inerentes do sistema, que modulam os efeitos dessas perturbações (Newman & Palmer 2003; Haynes 2009). Esse segundo componente recebeu até o presente atenção desproporcionalmente menor quando comparado ao primeiro (Roopnarine *et al*. 2007). Nesse sentido, o próximo passo para entendermos a extinção da megafauna do Pleistoceno é investigar se as comunidades do Pleistoceno poderiam ter colapsado, em parte, devido às suas propriedades estruturais, isto é, a forma com que as interações entre espécies estavam organizadas (Forster *et al*. 2003).

A organização das interações ecológicas e suas consequências dinâmicas em um dado local são objeto de interesse da teoria de redes ecológicas (Dunne 2006). Desde o debate sobre a relação entre estabilidade e diversidade desencadeado pelos estudos de Robert May demonstrou-se que a dinâmica de comunidades ecológicas, mais especificamente a resposta a perturbações, pode ser modulada pela forma como as interações entre as espécies estão organizadas (May 1971; Pimm 2003; Allesina & Tang 2012; Rooney & McCann 2012). Dessa forma, compreender a estrutura gerada pelas interações em uma comunidade ecológica e o papel dessa estrutura na dinâmica do sistema é fundamental para entendermos episódios de extinção biológica e, de maneira geral, os mecanismos que organizam a diversidade.

Reconstruir redes de interação do passado e avaliar as hipóteses sobre grandes extinções representa um grande desafio, uma vez que é impossível realizar observações e experimentação nesses sistemas. A reconstrução das redes de interação depende de inferências sobre as possíveis interações a partir de dados paleontológicos, baseando-se, por exemplo, nas relações biométricas entre as espécies (Fariña 1996; Prevosti & Vizcaíno 2006), estudos de isótopos estáveis (Coltrain *et al*. 2004, Yeakel *et al*. 2013) e estudos de espécies atuais supostamente análogas em seu modo de vida (Corlett *et al*. 2013). Informações sobre a ecologia da mastofauna africana atual, por exemplo, são comumente utilizadas para inferências sobre a paleoecologia da megafauna pleistocênica de outros continentes (Owen-Smith 1987; Guimarães *et al*. 2008). De fato, sob a premissa de que comunidades formadas por espécies similares obedecem a regras similares, se formos capazes de compreender os mecanismos responsáveis pela estrutura de redes de interações entre espécies atuais seremos capazes de inferências mais acuradas sobre as interações entre espécies extintas.

Informações sobre os mecanismos responsáveis pela organização das interações em comunidades atuais tem sido obtidas por meio do uso de modelos de teias alimentares (Stouffer 2010). Modelos de teias alimentares são conjuntos de regras capazes de gerar redes teóricas de interação (Williams & Martinez 2000). Diferentes modelos de teias alimentares baseados em regras simples de interações entre espécies são capazes de reproduzir a estrutura de redes de interações reais e, portanto, devem capturar parte dos mecanismos fundamentais que organizam essas redes (Williams & Martinez 2000, 2008; Cattin *et al*. 2004; Allesina *et al*. 2008).

Modelos de teias alimentares são particularmente úteis na reconstrução redes de interações entre espécies extintas. Por mais que as características biomecânicas e indícios fósseis sugiram a interação entre duas dadas espécies extintas, há sempre um alto grau de incerteza quando comparado a sistemas atuais, uma vez que o registro empírico das interações não é possível (Roopnarine *et al*. 2007; Dunne *et al*. 2008). Além disso, interações ecológicas podem ocorrer devido a características locais específicas ou devido a um conjunto de condições temporárias (Thompson 2005). O uso de modelos permite a simulação de diversos cenários possíveis com um mesmo conjunto de espécies, mantendo as características fundamentais da rede de interações, o que evita que as propriedades dessas redes estejam relacionadas a idiossincrasias de uma configuração arbitrária.

Os modelos de teias alimentares foram originalmente propostos para teias alimentares completas que contemplam vários níveis tróficos desde produtores até decompositores (Dunne 2006). Todavia, teias alimentares completas podem ser subdivididas em subredes que representam as interações entre espécies em dois níveis tróficos contíguos (Kondoh 2010). Nessas subredes há dois conjuntos de espécies, um representando consumidores e outro recursos não havendo interações entre os componentes do mesmo conjunto. Redes como essas, representadas por dois conjuntos bem definidos de elementos, são chamadas de redes bipartidas. Tais recortes de redes maiores levam algumas vantagens sobre teias alimentares completas: (i) em geral redes bipartidas possuem boa resolução taxonômica evitando problemas da incongruência na resolução entre os grupos (Polis 1991; De Visser *et al.* 2009); (ii) em redes bipartidas todas as conexões referem-se ao mesmo tipo de interação ecológica e estão presumivelmente sujeitas aos mesmos processos ecológicos e evolutivos (Lewinsohn *et al.* 2006). Essa subdivisão é evidente em comunidades compostas por grandes mamíferos uma vez que tais comunidades se comportam como compartimentos bem definidos das teias alimentares, com uma estrutura e dinâmica característica (Holt *et al.* 2008; Terborgh & Estes 2010). Pelos motivos acima focamos aqui em interações consumidor-recurso entre dois níveis tróficos. Entretanto, um primeiro passo para a reconstrução das redes do passado usando modelos de teias alimentares foi a adaptação dos modelos tradicionais ao caráter bipartido das redes consumidor-recurso.

Uma característica compartilhada pela maioria dos modelos de teias alimentares é a existência de uma hierarquia alimentar. Desde que os primeiros modelos de teias alimentares foram propostos (Cohen *et al.* 1990) o tamanho corpóreo tem sido considerado um forte candidato para explicar as regras de hierarquia alimentar e ordenação das espécies em que se baseiam os modelos (Warren & Lawton 1987; Allesina *et al.* 2008). De fato, diversas linhas de evidência sugerem que a massa corpórea seja uma característica adequada para a parametrização dos modelos, uma vez que, em geral, o tamanho dos organismos limita suas possibilidades de interação (Woodward *et al.* 2005; Brose 2010; Stouffer *et al.* 2011). Portanto, a parametrização dos modelos usando dados de tamanho corpóreo deve ser um caminho para modelos capazes de gerar redes teóricas mais realistas.

Uma vez que redes com estrutura realista possam ser reconstruídas é possível descrever a estrutura do sistema e utilizar diversas abordagens para compreender a sua dinâmica. Uma questão relevante do ponto de vista da dinâmica de um sistema ecológico é como esse sistema responde a perturbações. A análise qualitativa de estabilidade é uma abordagem que permite avaliar a resposta de sistemas dinâmicos a perturbações (May 1971; Allesina & Tang 2012). Apesar de restrita ao efeito de pequenas perturbações, a análise de estabilidade permite uma primeira avaliação do comportamento dinâmico do sistema (Pimm 2003; McCann 2011). Contudo, perturbações podem ter efeitos que se propagam por toda a rede de interações, por meio de interações diretas e indiretas entre as espécies, e levam à reestruturação da rede devido a extinções. Uma forma adicional para entender como comunidades respondem a perturbações de diferentes naturezas é simular a dinâmica do sistema por meio de modelos de dinâmica populacional (e.g., Alroy 2001). Simulações permitem avaliar as possíveis trajetórias das populações após a perturbação e identificar aquelas espécies que se extinguem e aquelas que persistem. Nesse sentido, a análise de estabilidade e simulações de dinâmica são duas abordagens complementares que permitem caracterizar a dinâmica do sistema de interesse e testar hipóteses sobre como o sistema responderia a diferentes fatores.

Os capítulos da presente tese representam os componentes de um esforço cujo objetivo final foi entender o papel da estrutura e dinâmica das comunidades do Pleistoceno no seu colapso. A tese está dividida em três seções: a primeira seção é composta por 2 capítulos que compartilham como motivação a adaptação de modelos de teias tróficas para redes bipartidas. Uma vez que os modelos de teias tróficas foram generalizados para reproduzir redes bipartidas, como as redes de interação predador-presa, foi possível utilizar os modelos para gerar redes de interação realistas entre os mamíferos do Pleistoceno, investigar como essas comunidades estariam organizadas e a dinâmica desses sistemas (seção II; Capítulos

3-5). Especificamente, busquei entender se particularidades da estrutura das redes do Pleistoceno podem explicar porque essas comunidades colapsaram, ao passo que as comunidades de grandes mamíferos da África persistiram. Por fim (seção III; Capítulo 6), apresento resultados relacionados às possíveis consequências da perda dos grandes mamíferos na América do Sul. Nessa última seção foco, especificamente, nos prováveis impactos das extinções sobre a dispersão de sementes, um serviço ecossistêmico com amplas implicações para a organização e funcionamento de sistemas naturais.

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SEÇÃO I

Adaptando modelos de redes ecológicas

CAPÍTULO 1

Do Food Web Models Reproduce the Structure of Mutualistic Networks?

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Abstract

Background: Simple models inspired by processes shaping consumer-resource interactions have helped to establish the primary processes underlying the organization of food webs, networks of trophic interactions among species. Because other ecological interactions such as mutualisms between plants and their pollinators and seed dispersers are inherently based in consumer-resource relationships we hypothesize that processes shaping food webs should organize mutualistic relationships as well.

Methodology/Principal Findings: We used a likelihood-based model selection approach to compare the performance of food web models and that of a model designed for mutualisms, in reproducing the structure of networks depicting mutualistic relationships. Our results show that these food web models are able to reproduce the structure of most of the mutualistic networks and even the simplest among the food web models, the cascade model, often reproduce overall structural properties of real mutualistic networks.

Conclusions/Significance: Based on our results we hypothesize that processes leading to feeding hierarchy, which is a characteristic shared by all food web models, might be a fundamental aspect in the assembly of mutualisms. These findings suggest that similar underlying ecological processes might be important in organizing different types of interactions.

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Introduction

A major challenge in ecology is to understand how ecological networks are assembled. Network assembly ultimately reflects how interactions between individuals of different species scale up to organize ecological communities [1,2]. The study of food webs, which are networks of trophic interactions among species, has benefited from the proposal of probabilistic, topological models that are able to reproduce the structure of trophic interactions by incorporating simple ecological processes (reviewed by Stouffer [3]). These models offer a way to build realistic food webs using a few parameters such as the number of interacting species and the number of interactions that can be estimated in the field [4,5,6,7]. By connecting the structure of real food webs with candidate underlying processes, such models provide a basis for investigating the implications of food web organization for ecological dynamics [8], species persistence [9,10], and ecosystem services [11]. Moreover, differences in how closely each model fits the structure of empirical food webs provide insight into the fundamental rules organizing trophic interactions in ecological systems [7,12,13].

The majority of studies on how such models reproduce ecological networks have focused on food webs, but there is an increasing body of theory that relies on probabilistic models to understand the structure of networks formed by other kinds of ecological interactions such as mutualisms [2,14,15,16]. The theoretical background for devising specific models for mutualistic networks stems from the fact that antagonisms and mutualisms differ in their fundamental ecological and evolutionary implications [17,18]. Additionally, mutualistic networks share some marked structural regularities that differ from antagonistic networks such as food webs [18,19,20]. For instance, mutualistic networks are best described as two-mode networks in which there are two sets of nodes (e.g., animals and plants) and there are no interactions among species within the same set [21]; in contrast, food webs are organized into several loosely defined trophic levels [12]. Moreover, mutualistic networks tend to be highly nested, that is, a given species interacts with a subset of the partners of species that have more interactions whereas antagonistic networks have lower degrees of nestedness [18,19](but see [22]). An additional feature of mutualistic networks is that they exhibit right-skewed distributions of the number of interactions per species [21], whereas in food webs, this skewness is, in general, less pronounced [23].

The well-established differences between food webs and mutualistic networks (e.g., [18,24]) have been counterbalanced by increasing evidence that ecological networks share some basic similarities. For instance, modularity, which was previously predominantly related to antagonistic networks [25,26], was reported in a large set of mutualistic networks [27]. Along the same lines, although nestedness is often higher in mutualistic than in antagonistic two-mode networks [18], a recent study [22] showed that food webs are actually composed of interconnected, nested, two-mode sub-webs.

Another way in which mutualistic networks and food webs converge is that most mutualistic relationships are, in fact, rooted in consumer-resource relationships [28,29]. For example, pollination is a type of mutualism that often involves animals foraging for resources provided by flowering plants [30]. Similarly, the frugivores that disperse seeds away from parental trees are usually foraging on fruit pulp [31]. Therefore, even though food webs and mutualistic networks differ in some key aspects of their structure, we should expect that ecological processes related to resource use partially shape these interactions in similar ways. In fact, all of the models proposed for food webs are inspired by processes shaping the consumer-resource interactions in a given locality. These consumer-resource interaction rules are quite general and may also apply to other types of interactions. In this sense, we hypothesize that food web models are able to reproduce the structure of mutualistic networks. To test this hypothesis we adapted food web models to reproduce two-mode networks and compared their performance, and that of a model designed for mutualisms, in reproducing real mutualistic networks. We first calculated summary statistics that described the structural properties of real food webs and used a likelihood-based model selection approach [32] in which we computed the likelihood of obtaining the observed values under a set of candidate network models. Finally, we explored whether simple topological features of mutualistic networks explain the performance of network models.

Methods

The models

To test the performance of food web models in reproducing the structure of mutualistic networks, we compiled a set of 10 pollination and 15 frugivory networks totaling 25 mutualistic networks (see Table S1 in supporting information). These networks ranged from networks with small species richness (animal species richness, $A = 14$; plant species richness, $P = 11$) to species-rich networks ($A = 64$; $P = 43$) and from loosely connected networks (connectance, $C = 0.07$) to highly connected networks ($C = 0.47$). For each of those networks, we generated an ensemble of 1000 matrices using four different models to test model performance. Whenever a model generated a network with disconnected species or with a C value 3% larger or smaller than the real one, we discarded that network before running the model again [5,33].

In most mutualistic relationships, interactions can only occur between species in two well-defined sets (e.g., animals and plants), but food webs do not have this two-mode structure. In this sense, in food web models, all species but producers can be both predator and prey; in contrast, animals in the mutualistic networks studied here (pollination and seed dispersal) act as foragers by feeding on fruits and nectar provided by plants. Therefore, we adapted all food web models used to the two-mode nature of mutualistic networks. Our objective was to make as few changes as possible in the original models. We used the same set of simple rules of food web models, but interactions only occurred among species of different sets. As a result, all of the models used the input parameters A and P as well as the connectance, which is defined as $C = E/AP$, where E is the number of recorded interactions. Below, we first describe each model in detail and then the adaptations we made to deal with the two-mode nature of mutualistic networks. We recognize that the models used in this study only represent a subset of the available food web models (e.g., [6,13,34,35]), but we consider this to be a representative set of models that encompass a wide range of candidate rules for how food webs are built up. Moreover, several models were proposed to explain the structure of mutualistic networks (e.g., [2,14,36]). However, because our focus is to build a bridge between models describing antagonistic and mutualistic relationships, we chose to compare food web model performance with that of a recent proposed model that was directly inspired by food web models and has been shown to successfully reproduce the structure of mutualistic networks [15].

The cascade model. The cascade model was the first of a series of static models that were capable of reproducing some of the structural properties of real food webs [4]. The cascade model is based on the assumption of hierarchical feeding, assigning each of the S species in the community a random value that is uniformly drawn from the interval [0,1], which represents species position along a one-dimensional feeding hierarchy (Fig. 1A). Each species has a probability $q = 2CS/(S-1)$ of consuming those species whose values are smaller than its own [5]. In our effort to adapt the cascade model to the two-mode nature of mutualistic networks, the position of species are assigned independently for animals and plants so that instead of ordering all species along an axis there are two axes: one for animals and the other for plants (Fig. 1B). Animals can potentially interact with plants whose values are smaller than their own but can never interact with other animals. The probability q of the original model was not valid for the two-mode version; we defined it as $q = E/T$, in which T is the number of possible interactions after species positions are defined. This approach ensures that the model creates networks with connectance that closely resembles the connectance of the empirical food web.

The niche model. The niche model addresses some of the limitations of the cascade model; in particular, it addresses the lack

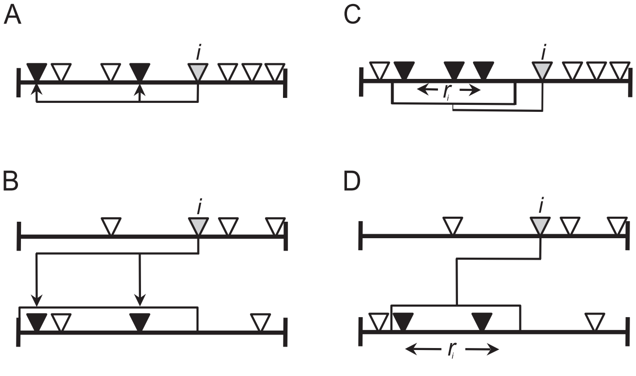

Figure 1. Diagrams comparing original food web models and their two-mode version. (A) the cascade model: each species (represented as an inverted triangle) is assigned a random value being placed along an axis. A given species *i* (gray) potentially interacts with those species whose values are less than the value assigned to *i* (as indicated by arrows); (B) the cascade model for two-mode networks: species that pertain to different sets (e.g. plants and animals) are randomly placed along two separate axes. The upper axis represents the axis of consumers. Therefore a given species *i* in the upper axis potentially interacts with those species in the lower axis whose values are lower than the value assigned to *i*. (C) The niche model: Each species is assigned a random value n_i and consume all species within a range of niche values r_i. (D) The niche model for two-mode networks: species that pertain to different sets (e.g. plants and animals) are placed along two separate axes according to their n_i. Each species in the upper axis consume all species in the lower axis that fall within a range of niche values r_i.
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of feeding cycles and cannibalism. However, the niche model retains much of the simplicity and tractability embodied by the earlier model [5,12]. As in the cascade model, the original niche model [5] assigns a position (n_i) taken from a uniform distribution on the interval [0,1] for all S species and places each of them along a gradient (Fig. 1C). For each consumer i, a niche range $r_i = xn_i$, where $0 \leq x \leq 1$ is a random variable with a beta-distributed probability density function $p(x) = \beta(1 - x)(\beta - 1)$ with $\beta = (1/2C) - 1$ is then defined. This causes species with higher n_i to tend to eat more species and ensures that the average of all species' r equals C [33]. The range center (c_i) is a uniformly random number between $r_i/2$ and min (n_i, $1-r_i/2$). A consumer i eats all species j whose n_j fall within its range (Fig. 1C). Hence, a diet interval $I(D_i) = [c_i - r_i/2, c_i + r_i/2]$ is defined for all species. As in the cascade model, to adapt the niche model to mutualistic networks, we defined n for plants and animals within two separate axes and diet ranges were defined only for animals and projected in the plants axis, such that animals always behaved as consumers and plants always behaved as food resources (Fig. 1D). Although we recognize that in many cases plant traits are responsible for selecting their interaction partners and thus network assembly could occur from the perspective of plants (e.g., [36]) we opted for an approach that is similar to the original models in which basal species have no defined ranges [5]. To obtain $I(D)$ for animals, we used functions that are identical to those used in the original model (see Text S1 for reasoning).

In addition to having a more complex set of rules, the niche model differs from the cascade model because it imposes intervality in how links to resource species are assigned. Intervality means that all of the species in a food web can be placed in a fixed order on a line such that each consumer's set of resources forms a single contiguous segment of that line. Therefore, intervality suggests that trophic niche space can be represented by a single dimension [12,37].

The minimum potential model. Even though the niche model seemed to perform fairly well in reproducing most of the features of empirical food webs, food webs often do not show intervality for all species [34]. The minimum potential niche model [7] is a niche-based model that relaxes the interval feeding constraint of the niche model in a similar way to the relaxed niche model [33]. In the minimum potential niche model (hereafter MPN), forbidden interactions lead to gaps in consumers' diets [7]. The MPN model can be seen as a way of embedding multidimensional niches into a one-dimensional context [7]. The MPN model is similar to the niche model in that at first, the positions along the niche axis and diet interval $I(D_i)$ of each species are defined. However a consumer eats species that fall within its diet interval with probability $1 - f$, where f is the probability of having forbidden links in the diet (see Text S2). To adapt the MPN model to mutualisms two axes are defined and only animals posses $I(D)$ as in the niche model.

Model of bipartite cooperation networks. The model of bipartite cooperation (hereafter the BC model) was conceived for two-mode cooperation networks such as mutualistic networks and was directly inspired by food web models [15]. Here, we used a slightly different version of the model described by Saavedra et al. [15], following the authors' suggestion. In this model, plants are treated as members of class P and animals as members of class A. The model consists of two mechanisms: specialization and interaction. The specialization rule determines the number of interaction partners, l_{pi}, of each species $p \in P$. This number is determined by the interaction among two values: the reward trait, t_{Rp}, a number randomly drawn from an uniform distribution [0,1], which is attenuated or amplified by an external factor λ_p that is randomly drawn from an exponential distribution, which accounts for effects such as population density. The higher the reward value of plant p_i, the higher is the number of potential interactions established by p_i. The interaction rule determines which species $a \in A$ interacts with each species $p \in P$. Interactions are limited by the complementarity between the reward traits, t_{Rp}, for $p \in P$ and foraging traits, t_{Fa}, for $a \in A$. The foraging trait $t_{Fa,}$ which are also uniformly drawn from [0,1], limits the range of possible partners for each member of class A, but again, interactions are affected by external factors $\lambda_{lp,}$ which could represent, for instance, temporal variation and population density that are randomly drawn from an exponential distribution for each interaction.

Interactions are distributed to plants sequentially, in ascending order, according to their foraging traits t_{Rp}. Whenever $t_{Rpi} > \lambda_{lpi}$ each link l_{pi} is connected to the first node $a' \in A'$, where A' is the subset of nodes in A that have not already been linked to by another node $p \neq p_i$. Conversely, if $t_{Rpi} \leq \lambda_{lpi,}$ interactions of p_i are distributed using a mechanism similar to that proposed by Cattin et al. [6], i.e., a plant $p \in P$ with lower trait value is randomly selected, and an interaction is established with an animal randomly chosen among its partners $a'' \in A''$ where A'' is the subset of nodes in A that have been linked in a previous time step. If the supply of nodes in either A' or A'' is exhausted before all l_{pi} links have been allocated, then nodes in the other subset are linked to instead. For additional detailed information on the model we refer readers to Saavedra et al. [15].

Performance analysis

For each empirical network and their theoretical counterparts, we calculated four structural properties often used to describe the structure of mutualistic networks: the degree of nestedness [19], degree of modularity [27] and the cumulative degree distributions for both animals and plants [21]. We then used two procedures, model fit and model likelihood, to evaluate the model performances in reproducing these structural properties. Below, we describe each structural property and both procedures to test model performances.

Nestedness. Nestedness is a property of networks in which the interacting assemblage of a species is a subset of the interacting assemblage of species with more interactions [19]. The index *NODF* (an acronym for nestedness metric based on overlap and decreasing fill [38]) was used to compute the degree of nestedness of both empirical networks and those generated by the models. *NODF* ranges from 0, when the matrix shows other nonrandom patterns of resource use, to 100, when the matrix is perfectly nested (additional information on *NODF* at [38]).

Modularity. Modules within a network are subsets of species that are more densely connected to each other than to species in other modules [39]. To find the best partition of a given network into modules, we used the simulated annealing algorithm to maximize and index of modularity, M, that accounts for the number of interactions between species belonging to the same module and the number of interactions between species belonging to different modules [39]. M equals 0 if nodes are placed at random into modules or if all nodes are in the same module and approaches 1 if modules have well-delimited boundaries (i.e., few between-module interactions). Although M does not take into account the fact that mutualistic networks are two-mode networks, any potential effect of the two-mode structure on modularity is controlled since all networks analyzed have two sets of species. Thus, any difference in M among real and theoretical networks cannot be related to the two-mode structure.

Degree distributions. The degree, k, of a species i in a mutualistic network can be defined as the number of species with which species i interacts. Therefore, the cumulative degree distribution of a mutualistic network describes the proportion of species with k or more interaction partners [21]. It can therefore be considered a description of the pattern of ecological specialization in the community [40]. Because we dealt with two-mode networks, degree distributions were calculated separately for animals and plants.

Model fit. To test whether the models were capable of reproducing empirical network properties, we used different procedures depending on the topological property analyzed. For nestedness and modularity, we calculated the normalized model error (*NME*) between the empirical values and the values obtained from the numerical simulations of each model. The *NME* can be defined as the difference between the model's median property value and the empirical value divided by the difference between the model's median property value and the property value at the 2.5% or 97.5% quantiles, depending on whether the empirical value is lower or larger than the model's median [33]. A value of *NME* greater than 1 means that the empirical value is significantly different from the degrees of nestedness or modularity of networks generated by a given model [33]. By doing this, we did not make particular assumptions about the distribution of property values generated by the food web model [33]. Here, we used a slightly modified version of *NME* in which we use the absolute value of the difference between the median and the quantile to normalize the index so that the direction of the deviation is maintained. Therefore, a positive *NME* indicates overestimation of a property value by the model, and a negative *NME* indicates underestimation. To test whether the models were capable of reproducing degree distributions, we used the Kolmogorov-Smirnov test [13].

Model likelihood. The procedures described above allow us to distinguish among situations in which a network property is reproduced or not. However one model could be regarded as the one with larger fit when in fact it just produces a larger variance of metric values. Therefore, to perform comparisons among models, we opted to use the likelihood approach, which is a statistical framework specifically designed to allow direct comparisons among many competing models [32]. Recent studies (e.g., [41,42]) aiming to describe how mutualistic networks change over time have shown that species pairwise-interactions are highly variable whereas the overall network structure often remains unmodified. Therefore, we opted for a likelihood approach that differs from recent proposed likelihood frameworks, which focused on finding the model that was most likely to reproduce all pair-wise interactions observed in real networks [7,43]. Because we were interested in the distinct overall structural properties of each network, the objective of our likelihood approach is to determine which model was most likely to reproduce the observed value for each property separately, gauged by a summary statistic (see [44]). If the difference between the negative log-likelihood of the best model and another given model was less than 2, they were considered equally plausible [32]. For additional information on how we computed model likelihood using simulations see Text S3.

Correlates of model performance. To develop a better understanding on which characteristics of the real network affects the performance of each model, we used a general linear model to test whether features such as connectance (C), animal species richness (A), plant species richness (P), and the nestedness and modularity values themselves affected the normalized errors of each model, *NME* (i.e., a proxy for the degree of fit of a given model for each real network). We used relative nestedness (N^*; [19]) and relative modularity (M^*), in which the observed value is corrected using the average value of 1000 random networks with the same size and connectance as the original network. The results still held if we assumed other theoretical benchmark that kept heterogeneity in the number of interactions across species ("null model 2", [19], Table S2). There was no correlation among N^* and M^* ($r = -0.39$, $n = 25$, $P > 0.05$), which allowed both to be included in the analysis as explanatory variables. Then, for each of the four models, we used multiple regression models of the following form:

$$NME = \beta_0 + C\times\beta_1 + A\times\beta_2 + P\times\beta_3 + N^*\times\beta_4 + M^*\times\beta_5 + \varepsilon$$

where *NME* is the normalized error, β_i are the coefficients of the multiple regression and ε is the usual Gaussian error. All regressions assumptions, such as the normality of residuals, were met. Then we used the Akaike criterion to select the best set of variables in predicting *NME* [45]. The tests were performed for *NME*s in reproducing *NODF* and *M* separately.

Results

All models performed remarkably well in reproducing both the nestedness and modularity of the mutualistic networks. The percentage of networks whose metrics were reproduced by each model varied between nearly 50% and 95% (Table 1). The models that reproduced the properties in the largest proportion of networks were the two-mode cascade model and the BC model (Table 1). When we directly compared the models as competing hypotheses using the likelihood approach, the outcome of the model comparison depended on the property being analyzed (Table 1). The cascade and niche models were among the most likely models for 84% of the networks considering nestedness. This result held when using a different nestedness metric, the matrix temperature, which indicates that these results are not affected by metric choice (Text S4). Similarly, when considering modularity, the cascade model was among the most likely models for 84% of the networks. However, the BC model instead of the niche model was the second best model in terms of reproducing modularity (Table 1). Regarding degree distributions, the results are less straightforward. All four models reproduced degree distributions for nearly all analyzed networks according to the Kolmogorov-Smirnov test results (Table 1). Nonetheless, the model comparison suggested that the cascade model was usually among the best models in reproducing plants degree distributions, whereas the niche and BC models outperformed the others more often in reproducing the degree distribution of animals (Table 1).

The sign of *NME* indicates whether the model overestimates or underestimates a property value for a given network. Therefore, an excess of negative values of *NME* indicates that a model often

Table 1. Proportion of mutualistic networks ($N = 25$) whose properties were reproduced by each model ($NME < 1$; $P_{KS} < 0.05$)/proportion of networks in which each model was among the most likely.

	NODF	*M*	Pk_A	Pk_P
Cascade	0.84/0.84	0.88/0.84	0.96/0.52	1.00/0.76
Niche	0.80/0.84	0.52/0.44	1.00/0.88	0.96/0.60
MPN	0.60/0.68	0.56/0.60	0.84/0.64	1.00/0.64
BC	0.72/0.80	0.80/0.72	0.96/0.84	0.92/0.60

Columns represent the network properties analyzed: *NODF* = nestedness, *M* = modularity, Pk_A = cumulative degree distribution of animals, Pk_P = cumulative degree distribution of plants. Because more than one model could reproduce or be among the most likely models in reproducing the property of a given network the sum of the proportions in each column is larger than 1.
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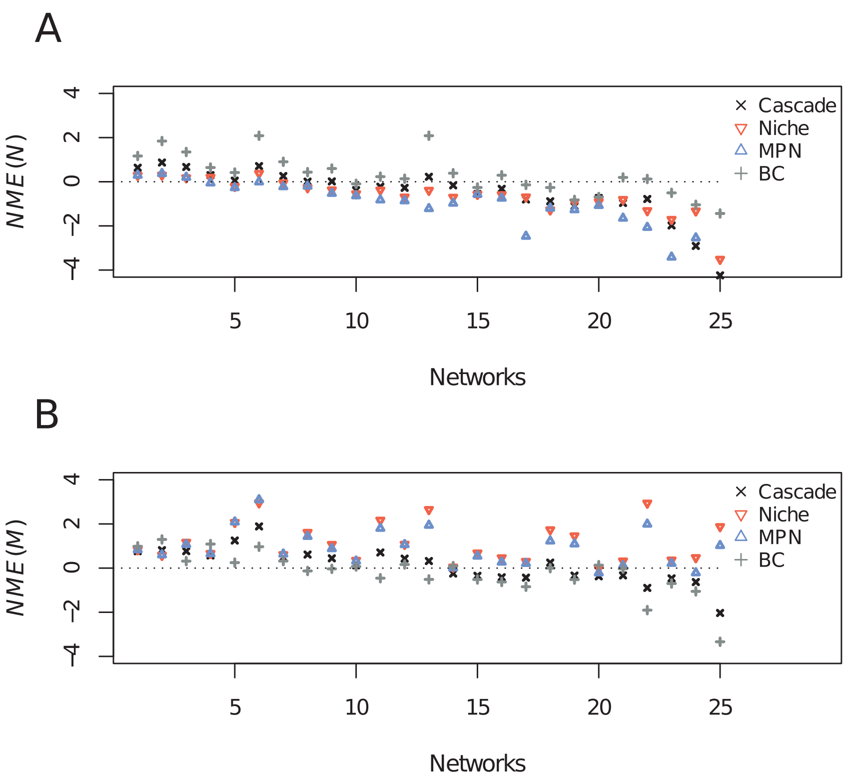

Figure 2. Normalized error (*NME*) of each model in reproducing nestedness (A) and modularity (B) for each of the 25 analyzed networks. In (A) networks are sorted in increasing order of relative nestedness. Notice nestedness tend to be underestimated for networks with large nestedness degrees as suggested by partial regression coefficients (Table 2). In (B) networks are sorted in increasing order of relative modularity.
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underestimates a given property, whereas positive values suggest that the model has a tendency to overestimate it. The niche and MPN models tended to generate networks with lower degrees of nestedness and higher degrees of modularity than real networks (Fig. 2). The cascade and BC models were more balanced and showed fewer signs of systematic biases in one direction or another (Fig. 2). However, the degree of fit of models was associated with basic topological features of networks (see Table 2). Noteworthy network basic features explained between 70 and 95% of variation in model fit regarding nestedness and modularity. All models tended to underestimate nestedness as the degree of relative nestedness observed increased ($P<0.01$; Table 2, Fig. 2A). The degree of relative nestedness also affected the ability of the cascade, niche and MPN models to reproduce modularity. These models tended to overestimate network modularity for networks that had a high degree of relative nestedness (Table 2). The degree of relative modularity had the opposite effect for the cascade, MPN and BC models. When reproducing networks with high

Table 2. Effects of basic real network features in model degree of fit as expressed by the *NME*.

	F	*df*	r^2	*A*	*P*	*C*	*N**	*M**
Cascade	266.4**	23, 1	0.92	–	–	–	−2.01***	–
Niche	67.1***	21,3	0.89	−0.01*	–	–	−1.05***	2.07*
MPN	241.5***	22,2	0.95	−0.01***	–	–	−1.84***	–
BC	19.11***	21,3	0.70	–	–	3.15**	−0.6***	4.12*
Cascade	31.54**	20,4	0.83	0.01*	–	1.6*	0.60***	−6.15***
Niche	40.5***	21,3	0.83	0.01**	–	−1.59*	0.76***	–
MPN	86.84***	22,2	0.87	0.01***	–	–	1.00***	–
BC	31.89***	22,2	0.72	–	–	2.53**	–	−8.34***

Multiple regression analyses results reporting the F-statistics (*F*), degrees of freedom (*df*), determination coefficient (r^2) and the partial regression coefficients of each of the following factors: animal species richness (*A*), plant species richness (*P*), connectance (*C*), relative nestedness (*N**) and relative modularity (*M**). Traces mean that the factor was not included in the best regression. The significance of each factor and the model as a whole is represented as follows:
*<0.05;
**<0.01;
***<0.001. The first 4 rows correspond to the *NME* for nestedness and the last for modularity.
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relative modularity, these models were more prone to underestimate modularity (Table 2). Connectance also affected model fit. Networks with larger connectance tended to have their degrees of modularity and nestedness overestimated by the cascade (only for nestedness) and BC models, whereas modularity *NME* decreased with increasing connectance for the niche model (Table 2).

Discussion

Our results show that all four models performed fairly well in reproducing the properties of empirical mutualistic networks. However, the cascade and BC models more often generated theoretical networks that were in agreement with the structure of real mutualistic networks. Moreover, the cascade model was frequently among the most likely candidate models in reproducing the structure of mutualistic networks. Although the performance of the cascade and BC models was similar, the cascade model is much simpler than the BC model. In addition to attributing a value to each species as done in the cascade model, the BC model has many other free parameters that act as external factors that affect interactions. Therefore, the good performance of the cascade model appears even better when model complexity is taken into account.

In food webs, the cascade model also reproduced some aspects of the structure of interactions between consumers and resources [5]. Nevertheless, other models such as the niche and MPN models often outperformed the cascade model in reproducing food web structure [5,7,33]. The niche model was mainly proposed as a solution that included the possibilities of feeding loops and cannibalism, which were not allowed by the minimal rules of the cascade model [12]. In plant-animal mutualisms, on the other hand, interactions only occur between species in different trophic levels (plants and animals that forage in plant resources). Therefore, as we dealt with this two-mode structure of mutualisms, feeding loops were not a problem. This may partially explain the success of the cascade model for mutualisms in spite of being outperformed by niche model derivatives in the context of food webs [5,7,33]. In addition to the two-mode structure, other biological aspects of mutualisms might explain why the strict feeding hierarchy generated by the cascade model suffices to reproduce much of the structure of mutualistic networks.

Hierarchy is also an essential component in the BC model, which was directly inspired by the set of rules of food web models [15]. The success of the BC model in reproducing network structural patterns in a previous work [15] already suggested that such hierarchical processes should play a crucial role in organizing mutualistic networks. Because all models considered here encompass hierarchical processes our results reinforce their relevance in mutualisms. Moreover, the similar success in reproducing the structure of real networks of both BC and the much simpler food web models suggest that the feeding hierarchy by itself is enough to capture much of the structure of mutualistic networks. Although multiple processes may generate similar patterns in ecological systems, our results at least indicate possible mechanisms shaping the organization of mutualistic interactions in networks of interacting species.

The most compelling biological basis proposed for the ordering dimension that induces a feeding hierarchy in food web models is body size [12,37,43,46]. In this sense, in the context of food webs, the hierarchical ordering in the cascade model would lead to larger species interacting with smaller species. Similarly, in niche models, larger species would tend to have wider trophic niches [43]. In the case of pollination and frugivory networks, such hierarchy could refer to any measurable traits related to the feeding interaction among fruiting/nectar-producing plants and fruit/nectar consumers such as bill diameter, bill or mouthparts length, and fruit size or corolla depth. Such traits would be represented in the adapted models as the two independent axes in which animals and plants are ordered. Indeed in a series of studies, Stang et al. [47,48] showed that structural patterns of pollination networks such as nestedness could be reproduced by incorporating size thresholds imposed by floral morphology on nectar-feeding animals. Moreover, body size was found to predict the number of interactions of ants in ant-plant mutualisms [49]. Finally, larger frugivores are often able to eat a large variation in fruit sizes than smaller frugivores, leading to hierarchical ordering in frugivory [31]. From an evolutionary perspective trait based feeding hierarchies can emerge as a consequence of natural selection favoring particular high profitable resource combinations [17].

The way each model encompass feeding hierarchies may also partially explain differences in model performance. Species-rich mutualisms often form networks modules of interacting species based on shared phenotypic traits such as fruit color, flower shape, animal body mass [27,50]. Nevertheless, modularity in mutualisms such as pollination and seed dispersal is often smaller than observed in antagonistic interactions [18] or in symbiotic mutualisms [2]. The strict feeding hierarchy imposed by the cascade model causes high overlap in the set of interaction partners among consumer species, leading to low modularity. Conversely the set of rules in other food web models, such as niche and MPN models, that partially relax the cascade hierarchy [9] might favor higher modularity. In niche and MPN model, species whose feeding ranges overlap may form network modules that differ from modules formed by species whose feeding ranges overlap farther in the niche axis. In fact, both niche and MPN models were outperformed by the cascade and BC models in reproducing the low degree of modularity in mutualistic networks, especially because they usually generated networks that were more modular than the empirical ones. This may also partially explain the superior performance of both the niche and MPN models in comparison with the cascade model in generating the more modular structure of food webs [5,33].

The degree of relative nestedness and relative modularity of the real network were the main features of real networks affecting model fit; for networks with higher relative nestedness, the cascade, niche and MPN models tended to underestimate nestedness and overestimate the modularity of real networks. Conversely for networks with higher relative modularity, real modularity was usually underestimated. The sensitivity of the models accuracy to the degree of nestedness and modularity in the real networks indicates that the high degrees of nestedness or modularity observed in some mutualistic networks are not completely explained by the processes incorporated in food web models analyzed here. Stouffer et al. [13] showed analytically that a food web model should satisfy two criteria in order to reproduce most empirical food web properties: niche values should form a totally ordered set, and each species has a specific, exponentially decaying probability of preying on a fraction of the species with lower niche-values. In the context of mutualisms, it seems that a model's ability to reproduce empirical networks is not only a matter of reproducing the functional forms for the distributions of numbers of prey, predators and links per species, but also of reproducing the relationship between nestedness and modularity. Many mechanisms have been proposed for the occurrence of the nested pattern, namely, differences in abundance among species [26,51], low interaction intimacy [2], trait complementarity and/or exploitation barriers coupled with coevolutionary convergence [14,17,48] and frequent extinctions of specialist-specialist interactions [52]. Along the same lines, trait matching along with phylogenetic constraints [20] and high interaction intimacy [2] are regarded as the main mechanisms that could lead to a modular structure in mutualistic networks [27]. The rules of the cascade, niche and MPN models can be interpreted as a form of encompassing trait complementarity and exploitation barriers among interacting species. Similarly, the BC model is based on the complementarity among plants reward traits and animals foraging traits. Although they do incorporate complementarity, they do not explicitly consider other mechanisms shaping network structure such as interaction intimacy, differential extinction and phylogenetic constraints. Evolving network models, models in which the number of species and interactions change over time, have also been shown to partially explain the structure of mutualistic networks [2,36]. Future studies combining the mechanisms present in these two different classes of models might provide additional insights in the organization of mutualistic networks.

To sum up, food web minimal models were capable of reproducing most of the mutualistic networks analyzed. Noteworthy, even the cascade model, the simplest among the models considered here, reproduced the structure of nearly the whole set of networks. Such results open the possibility that the assembly of networks that describe mutualisms and antagonisms obey a similar simple set of rules and reinforce that feeding hierarchy might be a fundamental piece in this puzzle. Therefore, despite the differences in ecology and evolution of mutualisms and antagonisms [17,18], they seem to share some key aspects. Our knowledge of the assembly of natural communities would benefit from future studies that scrutinize those commonalities and differences and attempt to sort out the evolutionary and ecological mechanisms that are responsible for each.

Supporting Information

Text S1 The probability distribution for X for niche and MPN models.
(DOC)

Text S2 Definition of f for the MPN model.
(DOC)

Text S3 Computing model likelihood.
(DOC)

Text S4 Results using the metric Nestedness Temperature (T).
(DOC)

Table S1 Information on analyzed networks.
(DOC)

Table S2 Effects of basic real network features in NME with different N^* and M^* calculations.
(DOC)

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Author Contributions

Conceived and designed the experiments: MMP PRG. Performed the experiments: MMP. Analyzed the data: MMP. Contributed reagents/materials/analysis tools: PIP. Wrote the paper: MMP PIP PRG.

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CAPÍTULO 2

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Interaction intimacy organizes networks of antagonistic interactions in different ways

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Interaction intimacy, the degree of biological integration between interacting individuals, shapes the ecology and evolution of species interactions. A major question in ecology is whether interaction intimacy also shapes the way interactions are organized within communities. We combined analyses of network structure and food web models to test the role of interaction intimacy in determining patterns of antagonistic interactions, such as host–parasite, predator–prey and plant–herbivore interactions. Networks describing interactions with low intimacy were more connected, more nested and less modular than high-intimacy networks. Moreover, the performance of the models differed across networks with different levels of intimacy. All models reproduced well low-intimacy networks, whereas the more elaborate models were also capable of reproducing networks depicting interactions with higher levels of intimacy. Our results indicate the key role of interaction intimacy in organizing antagonisms, suggesting that greater interaction intimacy might be associated with greater complexity in the assembly rules shaping ecological networks.

1. Introduction

The ways in which species interactions are organized within biological systems affect different aspects of ecological and evolutionary dynamics, from community stability [1,2] to ecosystem functioning [3] and coevolution [4]. Ecologists have made substantial efforts to describe the structure and understand the assembly of ecological communities. Through these efforts, studies focusing on the biological attributes shaping species interactions have distinguished the key role of a few species traits in shaping patterns of interaction within ecological networks. These traits include abundance [5,6], interaction type [7] and interaction intimacy, the degree of biological integration among interacting individuals of different species [8–10].

There is compelling evidence that the degree of interaction intimacy shapes the ecology and evolution of species interactions [11]. High-interaction intimacy is often associated with the propensity of an individual to interact with few individuals of other species during most of its lifetime [8,11]. For example, in interactions established by symbiotic organisms, e.g. parasites and gall-forming insects, each individual spends a substantial part of its life within or attached to a single host. These interactions often involve a high degree of physiological integration associated with trophic and physical dependence. High intimacy at the individual level does not necessarily imply in high specialization at species level, as is well known for some generalist parasites [12]. Nevertheless, owing to the high level of biological integration between individual consumers and their hosts, extreme patterns of specialization, such as monophagy [13], are a common feature of some high-intimacy interactions. In contrast, interactions with lower levels of intimacy, such as those between predators and prey [14], often imply an absence of physiological integration or trophic and physical dependence on any single individual interaction partner. For mutualisms, the analysis of networks describing species interactions with different levels of interaction intimacy shows that these networks possess distinct structural properties that might be a result of distinct ecological and evolutionary dynamics [9,15]. Recent analyses also suggest that interaction intimacy is particularly important in shaping mutualisms, whereas the effects of interaction intimacy on the network structure of antagonisms are less clear [10].

A fundamental question is how the underlying processes moulding ecological networks differ between interactions varying in their degree of intimacy. Food web theory provides a useful approach to explore the potential differences between the assembly rules of antagonisms showing low- and high-intimacy interactions. The development of models capable of reproducing the structure of food webs [16] has yielded insights into the formative processes underlying ecological interactions [17–20]. Despite the simplicity of such models, the fit of a particular model to data suggests that it captures at least the most essential mechanisms of network assembly. Such food web models were originally developed to reproduce food webs that describe interactions across different trophic levels. However, recent work adapted these models to explore the mechanisms shaping two-mode ecological networks, such as plant–animal interactions [21,22].

This paper investigates the differences in the assembly rules of ecological networks related to interaction intimacy. We divided our analysis into two parts. First, we investigated the role of interaction intimacy in shaping patterns of interaction in antagonisms, such as parasitism, predation and variable types of plant–herbivore interactions. We expected that highly intimate interactions would have higher modularity due to different factors associated with the phenotypic integration among partners, including strong phylogenetic constraints and coevolution favouring specialization [9,23]. In contrast, high nestedness and low modularity are expected for interactions with low intimacy, in which differences in abundance [6] and body size [14] are hypothesized to play a key role. Second, the approach based on food web models allowed us to investigate whether the assembly of two-mode antagonistic networks varies across distinct levels of interaction intimacy. We tested the hypothesis that models with more complex rules would be required to reproduce networks with high levels of interaction intimacy.

2. Methods

2.1. The dataset and the characterization of interaction intimacy

To test if antagonistic networks with varying levels of interaction intimacy show different structural patterns related to different assembly rules, we used 26 two-mode antagonistic networks available online from the Interaction Web Database and compiled from the literature (see the electronic supplementary material, appendix A). This dataset encompass a broad range of antagonisms, including parasitism, predation, grazing and different types of plant–herbivore interactions, with networks ranging from small networks with no more than 16 species and 15 interactions to large networks with more than 300 species and 700 interactions (see the electronic supplementary material, appendix A). As in any dataset of ecological networks, certain types of interactions are under-represented (e.g. few aquatic antagonisms). However, we attempted to minimize the over-representation of particular types of interactions, such as parasite–host interactions, opting for a smaller dataset encompassing representatives of a variety of antagonisms. We did not use entire food webs because they often include different types of interactions varying in their degree of intimacy [16]. Conversely in two-mode networks all links represent the same kind of ecological interaction and thus are presumably subjected to similar ecological and evolutionary processes [23]. Moreover, we did not analyse networks in which a considerable proportion of nodes (‘species’) are actually sets of species that are assumed to be ecologically similar because two species sharing similar resources or consumers may differ strongly in their degree of intimacy. Although the preponderance of plant–herbivore networks in our dataset can be viewed as a potential bias, it is important to note that insects represent much of the animal diversity worldwide as well as most of the lifestyles found in nature [24].

Interaction intimacy can be viewed as a function of the degrees of physiological integration, trophic and physical dependence of interacting individuals of different species [8]. We opted to use a conservative approach [10], classifying each interaction according to three levels (low, intermediate and high) of interaction intimacy. Interactions with low intimacy ($n =$ eight networks) are characterized by an absence of physiological integration and physical dependence and by highly mobile consumers that are able to feed upon many different individual prey throughout their lifetimes. Examples include predation, grazing by mammalian herbivores and interactions between plants and leaf-chewing insects, such as grasshoppers. Interactions with intermediate intimacy ($n =$ eight networks) are characterized by an absence of physiological integration and a certain degree of physical and trophic dependence. Examples include the interactions between plants and insect herbivores whose individuals feed mainly in one or a few individual hosts for long periods of time, such as the larvae of lepidopterans, coleopterans and dacine fruit flies. Finally, interactions with high intimacy ($n = 10$ networks) are characterized by extreme physiological integration and the physical and trophic dependence of consumers on single hosts for at least part of the consumer’s life cycle, such as fish parasites, gall-forming insects, leaf-mining insects and endophagous flower parasites.

2.2. Structural analysis of antagonistic networks

We used six metrics to characterize the structure of antagonistic networks: (i) connectance, the proportion of all possible interactions that are actually recorded; (ii) variance in the number of interactions among consumers, σ_c^2 (iii) and among prey (hosts), σ_r^2; (iv) nestedness; (v) modularity; and (vi) the number of modules. We used the metric *NODF* (nestedness metric based on overlap and decreasing fill) to characterize nestedness [25] and *M* to characterize modularity and compute the number of modules in the network [26]. We used general linear models (GLMs) to investigate if interaction intimacy (coded as an ordinal explanatory variable) explains differences in each of the structural metrics. Because species richness varies widely across networks potentially affecting network structure, we used the total species richness, *S*, as a covariate. Network metrics are often correlated, for that reason, we performed two complementary analyses. First, we used a principal component analysis (PCA) to test whether the combined information on the metrics provides a clear partition among interactions with different levels of intimacy (electronic supplementary material, appendix B). Second, we used null model analysis to determine if the differences in nestedness and modularity are consistent after controlling for other network properties (see the electronic supplementary material, appendix B).

2.3. Food web models and assembly rules of antagonistic networks

To test whether networks with different degrees of intimacy are better reproduced by different assembly rules, we compared the ability of three probabilistic food web models, namely the cascade model [17], and the one-dimensional and two-dimensional probabilistic niche models (PNMs), respectively [27], to predict interactions within networks. Each model represents distinct candidate assembly rules with increasing degree of complexity that may reproduce antagonistic networks.

The first model is a probabilistic version of the cascade model [17]. In the original cascade model, each species is given a position (n) along an axis that represents a feeding hierarchy, and a given species i can only use species j as a resource if species j occupies a lower rank in the feeding hierarchy, i.e. if $n_i > n_j$. Because likelihood-based methods require that any interaction must have a non-zero probability of occurrence, we adapted the cascade model as a logit regression

$$\log\left[\frac{P(a_{ij}=1)}{P(a_{ij}=0)}\right] = \alpha + \beta\phi_{i,j}, \tag{2.1}$$

in which a_{ij} is a cell in the matrix $\mathbf{A}$ that depicts species interactions, α and β are parameters to be estimated, and $\phi_{i,j}$ equals 1 if $n_i > n_j$ and 0 otherwise. Thus, the probability of an interaction between consumer i and resource j given a particular parameter set $\theta = \{n_1, n_2 \ldots n_S, \alpha, \beta\}$ is

$$P(i,j|\theta) = \frac{\mathrm{e}^{\alpha+\beta\phi_{i,j}}}{1+\mathrm{e}^{\alpha+\beta\phi_{i,j}}}. \tag{2.2}$$

To maintain consistency with the original rules of the cascade model, we constrain α to be <1 and $\beta > 1$ such that the probability of interaction is larger if $n_i > n_j$.

In the probabilistic niche model (PNM) [27,28], the consumer may use a set of resources within a determined diet range. The probability of an interaction between consumer i and resource j is a continuous function:

$$P(i,j|\theta) = v\prod_{d=1}^{D}\exp\left\{-\left(\frac{n_{d,j}-c_{d,i}}{r_{d,i}/2}\right)^{\gamma}\right\}, \tag{2.3}$$

where $n_{d,j}$ represents the position in the niche dimension d for resource j, $c_{d,i}$ represents the diet optimum of consumer i for dimension d, $r_{d,i}$ is the diet range for consumer i within dimension d, γ controls the cutoff rate of the probability function and v is the maximum probability that i consumes any given prey, here set to 1 following Williams & Purves [27]. Because species in two-mode networks will only be consumers or resources, species positions (n) are defined only for the R species that are used as resources, whereas diet positions and ranges (c and r) are defined only for the C consumer species. Thus, the parameter set can be defined as $\theta = \{n_{d,1}, n_{d,2}, \ldots n_{d,R}, c_{d,1}, c_{d,2}, \ldots c_{d,C}, r_{d,1}, r_{d,2}, \ldots r_{d,C}, \gamma\}$. We restrict our analyses to the one-dimensional ($D = 1$) and two-dimensional ($D = 2$) niche models.

For each two-mode network represented by a matrix $\mathbf{A}$, we computed the probability of reproducing each link under each model (cascade, one- and two-dimensional PNMs) for a given set of parameters. Therefore, we define the log-likelihood for a given parameter set as

$$L(\theta|\mathbf{A}) = \sum_i\sum_j \ln\left\{\begin{array}{ll} P(i,j|\theta) & \text{if } a_{ij}=1 \\ 1-P(i,j|\theta) & \text{if } a_{ij}=0 \end{array}\right\}. \tag{2.4}$$

The maximum-likelihood parameter set is that which maximizes the likelihood. All models have a large number of parameters. Therefore, to obtain maximum-likelihood estimates (MLEs) is an optimization problem. We used simulated annealing [29], an optimization procedure that is less prone to become trapped in suboptimal values, and the Latin hypercube, a sampling technique that allows to explore large parameter space [30]. We repeated the procedure 30 times for each combination of networks and models, starting from different points in parameter space to improve the reliability of the estimates.

To compare model performance, we used the corrected Akaike information criterion for finite sample sizes, AICc [31]. The model with the lowest relative value of AICc is that showing the best fit to the data. We also computed the expected fraction of correct links for each network under each model, an additional measure of model performance [32]. The expected number of correctly predicted links can be computed as $N_\mathrm{c}(\mathbf{A}|\theta) = \sum_i\sum_j a_{ij}P(i,j|\theta)$. Therefore, the expected fraction of links predicted correctly, f_c, is obtained by dividing N_c by the number of interactions in the actual network. This approach is possible because MLEs for parameters imply that all models would tend to generate networks with connectances similar to the connectances of the real networks. We then tested whether the f_c differed between networks with high, intermediate and low intimacy. To control for the possible effect of network size on f_c, we used a GLM in which total species richness and level of interaction intimacy were factors. We performed the test separately for each food web model.

3. Results

After controlling for species richness, all aspects of antagonistic network structure but the variance in the number of interactions per consumers ($F_{2,23} = 1.36$, $p = 0.28$) varied across the gradient of intimacy in predictable ways: low-interaction intimacy was associated with higher connectance ($F_{2,23} = 5.74$, $p = 0.01$), higher nestedness ($F_{2,23} = 9.89$, $p = 0.0009$), a higher variance in the number of interactions per resource ($F_{2,23} = 17.36$, $p < 0.0001$), lower modularity ($F_{2,23} = 5.79$, $p = 0.01$) and a smaller number of modules ($F_{2,23} = 3.56$, $p = 0.04$; figure 1). In all cases, only networks with low intimacy differed significantly from networks with intermediate and high intimacy (figure 1). PCA analysis corroborates these results; by showing low-intimacy interactions structurally differ from networks formed by interactions with average and high levels of intimacy. Along of the same lines, null model analysis used to evaluate nestedness and modularity significance led to similar results, in which low intimacy is associated with significant nestedness and high and intermediate intimacy with significant modularity. For additional details on the analyses using the GLM, PCA and null model analysis, see the electronic supplementary material, appendix B.

The disparate structural patterns between antagonisms with low intimacy and higher degrees of intimacy produced differences in the model fit for networks depicting interactions with different levels of intimacy. The fraction of links correctly predicted by the cascade model (figure 2) was significantly higher for the low-intimacy networks (on average 76 ± 21%) than for the intermediate- (36 ± 20%) and high-intimacy networks (41 ± 26%, $F_{3,22} = 6.27$, $p < 0.01$). There were no significant differences in the performance of the one-dimensional PNM (low: 78 ± 20%; intermediate: 70 ± 23%; high: 78 ± 19%; $F_{3,22} = 0.39$, $p = 0.67$) and the two-dimensional PNM (low: 81 ± 20%; intermediate: 86 ± 10%; high: 88 ± 11%; $F_{3,22} = 0.41$, $p = 0.31$) models across networks depicting interactions with different levels of intimacy. The model selection procedure favoured different models for networks with different degrees of intimacy. The goodness of fit of the cascade model was the largest for six of the eight low-intimacy networks (figure 2). For intermediate and high levels of intimacy, the performance of the one-dimensional PNM was superior, showing the highest fit to the data for six of the eight intermediate-intimacy networks and six out of 10 of the high-intimacy networks (figure 2).

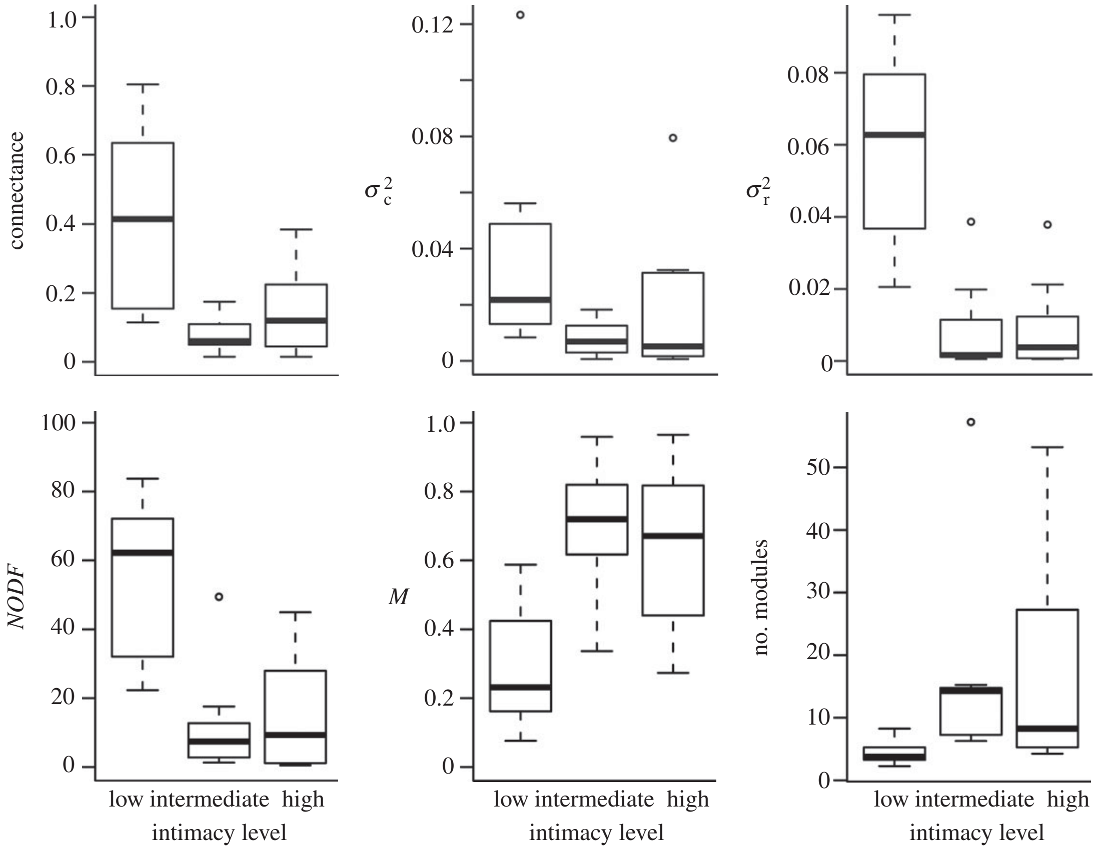

Figure 1. Boxplots for each structural metric of networks with different levels of interaction intimacy. The metrics are connectance; variance in the number of interactions among consumers, σ_c^2; variance in the number of interactions among resources, σ_r^2; nestedness, *NODF*; modularity, *M*; and the number of modules per network. The upper and lower limits of the box are the quartiles, the black band within a box represents the median and the error bars equal ±1.5 times the interquartile range.

The goodness of fit of the two-dimensional PNM was only larger for the largest intermediate-intimacy network and for one of the largest high-intimacy networks (figure 2). However, for large networks the differences in the AICc between the two-dimensional PNM and the other two models were generally smaller and the disparity in the fraction of links correctly predicted was generally larger (figure 2).

4. Discussion

Our results showed clear differences between the structural properties of networks depicting low-intimacy antagonistic interactions and those of networks that depict antagonistic interactions with intermediate and high levels of intimacy. A long-lasting notion is that high modularity and low nestedness characterize antagonistic ecological networks [7,23]. Here, we show antagonisms can give rise to nested networks when interactions have a low degree of intimacy. At the community level, the presence of generalist lifestyles in interactions with low intimacy produced not only lower specialization (higher connectance), but also higher nestedness. In contrast, the higher-intimacy interactions are associated with high specialization (lower connectance) and also to higher modularity in antagonisms. Similar patterns were reported for mutualisms, in which intimate mutualisms are highly modular, whereas low-intimacy mutualisms are often highly nested [9]. Taken together, these results suggest the ecological and/or coevolutionary processes that shape interaction patterns might be similar for systems with similar levels of intimacy despite these systems representing antagonisms or mutualisms. Nestedness partially emerges due to differences in population abundances among potential partners [6], probably a key component shaping both mutualisms and antagonisms with low intimacy. In addition, it has been proposed that grazing and free-living mutualisms might be much alike in the evolutionary processes shaping specialization [11], whereas symbiotic mutualisms might be similar to symbiotic antagonisms in the evolutionary processes shaping their patterns of interaction [33]. Moreover, our results suggest that interaction intimacy might have strong implications for the stability of species interactions. Nested patterns of resource use may have a destabilizing effect on antagonisms, as suggested by numerical simulations [7] and qualitative stability analysis [2], whereas the lower connectance and higher modularity of intimate antagonisms are associated with higher stability at the community level [2,7]. Future studies should investigate if antagonisms with low-interaction intimacy in fact tend to be more unstable to ecological perturbations than intimate antagonisms. Overall, our analyses using food web models contribute in three principal ways to our understanding of the organization of antagonisms involving multiple interacting species.

First, our results show that simple models are capable of reproducing different types of antagonistic, two-mode networks. Therefore, large differences in network structure can be reproduced by a set of simple models assuming that antagonistic interactions are determined by a few dimensions in the niche space. Because two-mode networks are the building blocks of more complex ecological networks [34], a

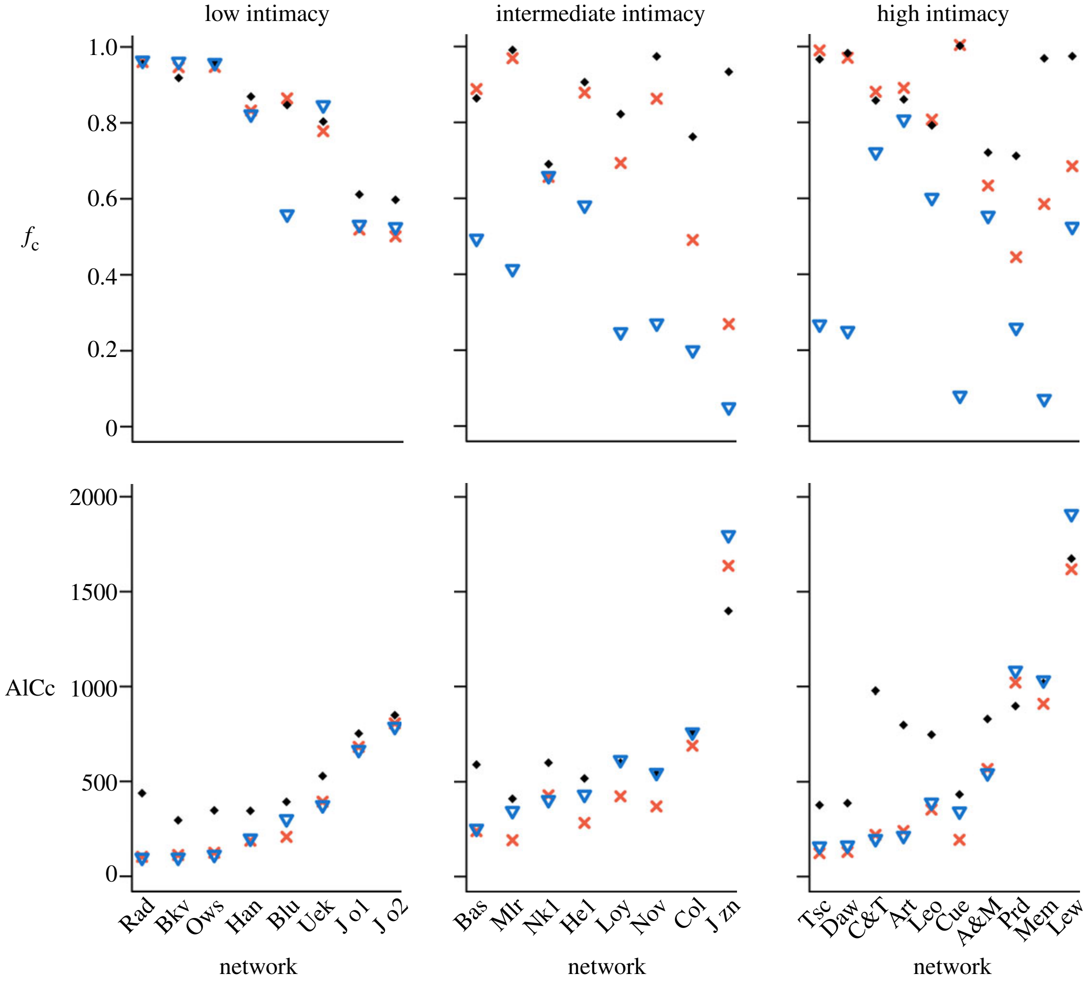

Figure 2. Fraction of correctly predicted links, f_c, and AICc values of each model for two-mode networks with different levels of intimacy. Networks are ordered from the smallest to the largest to highlight the effect of network size. Triangles represent the values for the cascade model, crosses for the one-dimensional PNM, and diamonds for the two-dimensional PNM. The name codes for each network can be found in the electronic supplementary material, appendix A. (Online version in colour.)

promising avenue for research is to explore how ecological networks formed by different types of interactions [10] can be reproduced by merging assembly rules in different ways.

Second, model performance differed among two-mode networks with different levels of interaction intimacy. The mechanisms underlying intimate interactions can be very complex. Organisms, such as leaf-mining and gall-forming insects and parasites need very specific host-recognition systems and mechanisms to avoid the mechanical and chemical defences of the hosts, in addition to specific morphology and physiology that allow these organisms to live within their hosts in such a close relationship [13,33,35]. Similar trends are observed in interactions with intermediate levels of intimacy, such as those formed by caterpillars and their host plants, in which complex defence/counter defence complementarities play a key role [36,37]. Thus, the assembly mechanisms of intimate interactions are in general much more complex than the mechanisms structuring low-intimacy trophic interactions, such as body size [14,32], feeding apparatus constraints [38] or phenological matching and abundance effects [39]. These differences were mirrored by differences in model performance. The cascade model, the simplest in the set of models we tested in this study, can reproduce a great percentage of the interactions in low-intimacy networks, but it performs poorly in reproducing networks depicting interactions with intermediate and high levels of intimacy. These results generalize recent findings [22] that the cascade model shows good performance in reproducing low-intimacy mutualistic networks, pointing out for general mechanisms shaping low-intimacy mutualisms and antagonisms.

The cascade model tends to generate networks that are more nested than modular [22] and was thus unable to reproduce the highly modular structure of networks of interactions with higher intimacy. Conversely, the two versions of the PNM were much more successful in reproducing the high-intimacy networks. The addition of one dimension to the niche space was only advantageous for the largest networks analysed. This finding agrees with previous results for whole food webs [27]. Therefore, the simple assumptions of the niche model appear to successfully capture the essential assembly rules of networks representing intimate interactions. The versatility of the rules of the niche model facilitates the reproduction of the patterns of interaction of consumers with very narrow diet ranges, allowing each consumer to explore a small portion of the feeding axis such that niche overlap is minimal. These results corroborate the view [40] that one-dimensional niche generalization may be a useful simplification in models used to reproduce the structure of food webs. Although this property certainly does not mean that only one characteristic of consumers and resources is important in determining who interacts with whom in a given locality [16], it does suggest that the core of the network of interactions is well represented by considering one dimension that can, in turn, represent a combination of traits. The current challenge is to find an approach allowing the different traits shaping high-intimacy interactions to be combined in estimates of the parameters. A next step in this analysis would be to parametrize these minimal two-mode models with biological information on species traits, as in the recently introduced body size-based models for entire food webs [28,32].

Third, in addition to the insights that they yield into the assembly processes of ecological communities, food web models furnish the possibility of building ensembles of networks that share the same realistic structural backbone but encompass the uncertainty of the occurrence of each pairwise interaction. For this reason, food web models have been used to build ensembles of food webs with a similar realistic structure. This approach allowed tests of the general properties of the structure and dynamics of study systems [2,41]. In this paper, we expanded the range of the types of ecological networks that can be reproduced by food web models. One key problem that still requires a solution is the extent of the applicability of the one-dimensional niche simplification results to all species and all their interactions. By probing into each network, future studies could provide an assessment of the species whose interactions are well predicted by food web models and the species for which food web models often fail. This assessment will allow us to improve our understanding of the generality of simple assembly rules and the complementary mechanisms generating the diversity of patterns of interaction in nature.

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SEÇÃO II

Estrutura e dinâmica de redes do Pleistoceno

CAPÍTULO 3

THE DISRUPTION OF PREDATOR-PREY INTERACTION NETWORKS AFTER MEGAFAUNAL EXTINCTIONS

Mathias M. Pires, Paul L. Koch & Paulo R. Guimarães Jr.

Abstract. The megafaunal extinction by the end of the Pleistocene drastically reduced the diversity of large mammals worldwide especially in the Americas. Considering the great chances in the composition of mammalian assemblages, it is expected this large extinction episode would have caused a major re-organization of species interactions, with implications to ecosystem function. However, we know little about how the communities these animals were part of were organized. We combine paleontological data and network models to reconstruct networks of predator-prey interactions between Pleistocene mammals in the Americas and investigate their structural properties. Although species composition were remarkably different between Pleistocene networks in America and modern large-mammal assemblages in Africa their network structure were likely similar. The Pleistocene extinction disrupted the structure of such networks so that large-mammal assemblages in the Americas are now simplified and more dependent on a few central species. Our results suggest that considering only the structure of Pleistocene assemblages there is no sign that they should be more prone to collapse them the assemblages we find today in Africa. Yet, we show Pleistocene extinctions in the America generated species-poor assemblages with structural properties that made them highly vulnerable to species loss.

INTRODUCTION

The extinction event known as the megafauna extinction, by the end of the Pleistocene (~50 – 11 kyr BP), drastically reduced the diversity of large mammals worldwide (Martin & Klein 1984). Australia and the Americas suffered the greatest impact with more than 70% of the mammalian genera extinct (Koch & Barnosky 2006). Although several hypotheses on the causes for the megafauna extinction have been debated (Koch & Barnosky 2006) we know little about how the communities that perished were organized, i.e., the structure formed by species interactions. The organization of ecological communities has implications for system dynamics and consequently for the systems properties such as robustness (Dunne 2006). Therefore understanding how ecological communities were organized may provide insights on the causes why a given system collapsed (Roopnarine *et al.* 2007). Nonetheless, to understand how paleocommunities were organized we need to find ways to reconstruct the patterns of interactions of extinct species, which is often challenging (Roopnarine 2009).

Evidences of paleoecological interactions such as marks of predators' teeth on the bones of prey (Marean & Ehrhardt 1995) or remains of food resources on the teeth of consumers (Akersten *et al.* 1988) are occasionally found. It is unfeasible tough to reconstruct the whole diet of a given species relying upon this type of evidence. When fossils are well preserved, stable isotopes can be used to estimate probabilities of interactions between pairs of species, allowing interaction patterns to be reconstructed from the isotopic profiles (Yeakel *et al.* 2013). Additionally, it is possible to make paleoecological inferences based on species biological traits. Dunne *et al*. (2008), for instance, compiled information on the possible trophic role of Cambrian taxa and aggregated taxa into trophic species to study the structure of networks describing the possible trophic interactions between Cambrian species.

An alternative for reconstructing paleoecological networks are modeling approaches (e.g., Roopnarine 2009). In studies with modern communities, food web models have been shown to reproduce several structural properties of real food webs (Williams & Martinez 2000; Stouffer 2010). Food web models are often used to build ensemble of food webs with a realistic structure, allowing network properties to be investigated (e.g., Brose *et al.* 2008; Dunne & Williams 2009). Here we combined this widely used approach in the study of modern food webs and paleontological data to investigate how Pleistocene mammal assemblages were organized. Understanding the structural properties of communities that collapsed is key to understand whether these communities had intrinsic properties that played a part in their collapse.

We first show network models can reproduce interaction patterns between large mammals that are currently observed in African ecosystems. Then, we use these models to reconstruct possible predator-prey networks between Pleistocene large mammals and investigate what would be the most likely structure of such paleoecological networks. To understand whether the organization of Pleistocene assemblages was as particular as their faunal composition we then compare the structure of Pleistocene networks with networks depicting interactions between the large mammals in Africa and the surviving large mammals in the Americas.

METHODS

Pleistocene Data

To build the Pleistocene predator-prey networks we gathered information on the composition of Pleistocene assemblages from the literature and the Paleobiology Database (http://paleodb.org/; Table 1 and Appendix S1). We searched for Pleistocene fossil assemblages for which the composition, chronology and taphonomy suggest an actual community of interacting species. Because we are interested in the interaction patterns of large Pleistocene mammals we considered only large predators, leaving out predators that were more likely to consume mostly small prey such as rodents and invertebrates. As prey we considered only mammalian herbivores weighing > 5 kg, which are more likely to be preyed upon by large carnivores (Carbone *et al.* 1999). We obtained data on the estimated body mass of extinct mammalian species from Smith *et al*. (2003b). When no body mass estimate was available for a given species, we used the average body mass of species within the same genus.

Reconstructing networks

Assuming similar large-mammal assemblages are organized by similar processes (Owen-Smith 1987), if a model is able to reproduce interaction patterns between African large mammals it should be appropriate to reconstruct Pleistocene networks with a realistic structure. Therefore, prior to the reconstruction of Pleistocene networks, we used data on the interactions between large mammals in three locations in Africa (Table 1) to test the performance of two different models in reproducing large-mammal predator-prey interaction patterns.

Although food-web models are often used in studies with whole food webs comprised of several trophic levels (Dunne 2006), food-web models can be adapted to reproduce networks of interactions between consumers and resources such as predator-prey interactions (Pires & Guimarães 2013). The first model is a parameterized version of the probabilistic niche model (PNM; Williams *et al.* 2010). Because body mass is often considered a key trait in determining species interactions (Brose *et al.* 2006), including predator-prey interactions between terrestrial mammals (Carbone *et al.* 1999), we parameterized network models using species body mass. In the PNM species are ordered along an axis representing a niche dimension and a predator preys upon species within a determined diet range along this axis. The probability of an interaction between consumer i and resource j is a continuous function:

$$P(i,j \mid \theta) = \nu \exp\left\{ -\left(\frac{n_j - c_i}{r_i} \right)^2 \right\} \tag{1}$$

where n_j represents the position in the niche dimension for prey j, c_i represents the diet optimum of predator i, r_i is the diet range for predator i, and v is the maximum probability that i consumes any given prey, here set as 1 following Williams *et al.* (2010). Because we are not considering intra-guild predation, species can be only predators or prey. Thus, species positions (n) are defined only for the prey species, whereas diet center and ranges (c and r) are defined only for the predators (Pires & Guimarães 2013). To parameterize the model using body mass information we followed Williams *et al.* (2010) and set $n = (\log m_j - \log m_{min})/(\log m_{max} - \log m_{min})$, where m_j is the body mass of prey species j and m_{min} and m_{max} are the minimum and maximum values for prey body mass. The parameters r_i and c_i are free parameters. Thus, the free parameter set can be defined as $\theta = \{c_1, c_2, \ldots c_P, r_1, r_2, \ldots r_P\}$.

The second model, herein LRM (log ratio model), is a statistical model that uses the log ratio of the body mass of predator and prey species as the explanatory variable (Rohr *et al.* 2010). The probability of interactions can be modeled as a logit regression:

$$\log\left[\frac{P(a_{ij} = 1)}{P(a_{ij} = 0)} \right] = \alpha + \beta \log\left(\frac{m_i}{m_j} \right) + \gamma \log^2\left(\frac{m_i}{m_j} \right) \tag{2}$$

in which a_{ij} is a cell in the binary matrix **A** that depicts species interactions. a_{ij} equals 1 if there is an interaction between predator i and prey j and 0 otherwise, and α, β *and*

γ are parameters to be estimated. Thus, the probability of an interaction between predator *i* and prey *j* given a particular parameter set θ = {α, β, γ} is:

$$P(i,j\,|\,\theta) = \frac{e^{\alpha+\beta\log\left(\frac{m_i}{m_j}\right)+\gamma\log^2\left(\frac{m_i}{m_j}\right)}}{1+e^{\alpha+\beta\log\left(\frac{m_i}{m_j}\right)+\gamma\log^2\left(\frac{m_i}{m_j}\right)}} \qquad (3)$$

For both models different parameter sets result in different probabilities of interaction. The maximum likelihood parameter set is that which maximizes the log-likelihood:

$$L(\theta\,|\,\mathbf{A}) = \sum_i\sum_j \ln\begin{Bmatrix} P(i,j\,|\,\theta) & \mathit{if}\ a_{ij}=1 \\ 1-P(i,j\,|\,\theta) & \mathit{if}\ a_{ij}=0 \end{Bmatrix} \qquad (4)$$

We combined the simulated annealing optimization (Kirkpatrick *et al.* 1983) and the Latin hypercube sampling technique (Mckay *et al.* 1979) to find the parameter set that maximizes the likelihood of each model (see Pires & Guimarães 2013 for a similar approach). To compare model performance, we used the Akaike information criterion, AIC (Burnham & Anderson 2002). The model with the lowest relative value of AIC is the one showing the best fit to the data. To provide a straightforward characterization of the performance of the models in reproducing each predator-prey network between African large mammals, we also computed the fraction of presences and absences of pairwise interactions (1's and 0's in matrix **A)** each model correctly predicts when parameterized with the maximum likelihood estimates:

$$f_c(\mathbf{A}\,|\,\theta) = \frac{\sum_i\sum_j a_{ij}P(i,j\,|\,\theta) + \sum_i\sum_j \left(1-a_{ij}\right)\left(1-P(i,j\,|\,\theta)\right)}{\sum_i\sum_j a_{ij}} \qquad (5)$$

By considering the ability of the model in predicting both the 1's and 0's in the interaction matrix we avoid overestimating the performance of a model that predicts, for example, that all interactions occur.

We also tested whether the models failed in any characteristic way for the three African predator-prey networks. A model parameterized with body mass could perform better in predicting the interactions of larger or smaller species or perform poorly in predicting the interaction of social hunters, for instance, which are more likely to take down larger prey then would be expected based on their body mass (Macdonald 1983). Thus, we computed an analogue of f_c for each species by fixing i (or j) in eq. 5 and dividing the numerator by number of interactions of i (or j).

Because both models performed similarly (see Results) we chose to use the LRM to reconstruct the Pleistocene networks. Even though the PNM has parameters that are easier to interpret biologically, such as preferred prey size and diet range, the LRM has far less free parameters than the PNM. As our main purpose here is not related to understanding the processes organizing interaction networks but to reconstruct networks with a realistic structure the LRM is, thus more appropriate. For each Pleistocene assemblage we generated 100 potential networks using the number of predators and prey and average body masses of each species as input parameters for the model. In each model run, we sampled the model parameters (α, β, γ) from the range defined by the maximum likelihood parameter set found for the three African networks. These parameters only determine how the probability of interactions are linked to body-mass ratios. As a consequence, variation in species richness and body mass distributions can lead to very distinct network structures even with the same parameter values.

Structural analyses

To describe network structure we focused on two structural properties: nestedness (Almeida-Neto *et al.* 2008) and modularity (Olesen *et al.* 2007). Nestedness and modularity are often found in two-mode networks including predator-prey networks (Pires & Guimarães 2013) and are important network patterns related to community dynamics (Bascompte 2010). Nestedness is high when the interactions of species with few interaction partners form a subset of the interactions of more connected species (Bascompte *et al.* 2003). We used the metric NODF (Almeida-Neto *et al.* 2008), to compute the degree of nestedness, herein N, of each predator-prey network. N tends to 100 for highly nested networks and to zero when species show other non-random patterns of interaction (Almeida-Neto *et al.* 2008). Network modularity is high when the network has groups (modules) of highly connected species that are loosely connected to other species in the network (Olesen *et al.* 2007). To find the partition of a given network into modules that maximizes within-module interactions relative to between-module interactions, we used an optimization algorithm to maximize an index of modularity, M (Guimerà & Amaral 2005). M tends to 0 when between-module interactions largely exceed within-module interaction, and equals $1\text{-}N_M^{-1}$ when the network contains N_M isolated modules. We used the program MODULAR (Marquitti *et al.* 2014) to compute M. Because each assemblage differs in the number of predators and prey and the number of species affect both nestedness (Almeida-Neto *et al.* 2008) and the number of modules (Olesen *et al.* 2007) we computed the relative nestedness and modularity to allow comparisons (Bascompte *et al.* 2003):

$$\begin{cases} N^* = (N - \overline{N}_R)/\overline{N}_R \\ M^* = (M - \overline{M}_R)/\overline{M}_R \end{cases} \qquad (6),$$

where N and M are the nestedness and modularity degrees of each network generated by the model and $\overline{N}_R$ and $\overline{M}_R$ are the average nestedness and modularity of random networks with the same number of species and same average number of interactions, where all interactions are equiprobable. With this null model approach we are not aiming to test the significance of structural patterns, but to control for the statistical effects of connectance and networks size on these metrics so we are able compare different systems.

Modern large-mammal assemblages in the Americas

A straightforward consequence of the Pleistocene extinctions was the reduction in the mammalian diversity. Yet, how these losses translated into changes in the structural properties, and ultimately dynamics, of mammalian assemblages is less clear. Thus, we used information on the interactions of extant large mammals in North and South America to explore the effects of the LQE over the network structure of large-mammal assemblages. Because in both North and South America there is not much variation in the composition of the few locations that still bear representative large-mammal faunas, we chose two locations to represent the surviving assemblages. We chose the Yellowstone Park, which bears one of the richest mammalian assemblages in North America (Van Valkenburgh 2001), and the Central region of South America, where the two extant large South American predators, the jaguar (*Panthera onca*) and the cougar (*Puma concolor*), can still be found in sympatry (Crawshaw & Quigley 2002). Using information on the diet of each carnivore (Taber *et al.* 1997; Crawshaw & Quigley 2002; Husseman *et al.* 2003; Smith *et al.* 2003a) we built the networks describing predator-prey interactions in each system. We excluded the coyote (*Canis latrans*), which was not considered in the Pleistocene assemblages as well, from the network representing North America, because it is known to include less live prey in its diets behaving more often as a scavenger (Smith *et al.* 2003a).

Network metrics that quantify the number of paths connecting species and how centralized are networks help us assessing how likely are the effects of perturbations to spread and how vulnerable is an ecological network to species loss. We used the average shortest path length and central point dominance, to measure the differences between the potential structure of Pleistocene and recent predator-prey networks. The number of connections between any two given nodes in a network is termed path length. The average shortest path, D, can be computed as the mean shortest distance between all pairs of nodes in the network (Williams *et al.* 2002). In ecological networks with smaller D species are tightly connected to each other and thus the effects of perturbations are more likely to spread (Williams *et al.* 2002). The central point dominance (CPD) is computed as:

$$CPD = \frac{1}{S-1}\sum_{i}\left(B_{\max} - B_i\right) \tag{7}$$

where $B_i = \sum_{j \neq i \neq k} \frac{l_{jk}(i)}{l_{jk}}$ is the betweenness centrality of species i (l_{jk} is the number of shortest paths from node j to node k and $l_{jk}(i)$ is the number of paths between j and k that pass through i); B_{max} is the largest value of betweenness centrality in the network and S is the total number of species (Costa *et al.* 2007). *CPD* is 0 if the network is totally connected and 1 when there is a central node (species) that participates in all interactions (Costa *et al.* 2007). Thus, *CPD* describes how dependent is the structure of an ecological network on a small subset of species. Because we are considering two-mode networks where only interactions between predators and prey are depicted, *CPD* will never reach zero, but will tend to zero if there are several nodes that are equally central.

RESULTS

Both network models performed well in reproducing the interaction patterns between African large mammals. Using only the number of predators and prey and their average body mass as input parameters, the models were able to predict on average more than 70% of the interactions correctly (Table 2). For two of the three networks the *LRM* had a better fit considering the number of parameters (Table 2). The LRM tended to perform slightly better in predicting the interactions of larger predators than smaller predators (Linear regression: $F_{1,12} = 4.78$, $R^2 = 0.22$, $p < 0.05$). The performance of the LRM was similar for social hunters, such as lions and wild dogs and solitary hunters, such as leopards and cheetahs. Regarding prey species, we found no trend related to body size ($F_{1,54} = 2.07$, $R^2 = 0.02$, $p = 0.15$) and although the model performed poorly (less than 50% of the interactions correctly predicted) in reproducing the interaction patterns of a few prey species (see Fig. S1 in Appendices) it did not seem to fail in any characteristic way.

Table 1. Sites included in the analyses, number of predators (N_{pred}) and prey (N_{prey}) and the average (± SD) degree of nestedness and modularity considering 100 potential networks reconstructed using the LRM. The values for African assemblages represent the actual values for the real interaction networks.

Site	Location	N_{pred}	N_{prey}	Nestedness	Modularity
American Falls (Amf)	Idaho, USA	7	15	79.82±4.09	0.13±0.03
Page-Ladson site -Aucilla River (Pls)	Florida, USA	5	15	75.48±4.87	0.13±0.03
La Brea Tar Pits - Pit 91 (Bre)	California, USA	8	12	78.62±6.20	0.16±0.03
Friesenhahn Cave (Fri)	Texas, USA	6	9	80.53±6.62	0.14±0.03
Ingleside (Ing)	Texas, USA	5	17	72.15±5.47	0.15±0.03
Guerrero Member – Luján (Luj)	Buenos Aires, Argentina	5	23	73.34±3.65	0.17±0.04
Talara Tar seeps (Peru)	Talara Region, Peru	3	9	61.92±8.99	0.11±0.04
São Raimundo Nonato (Srn)	Piauí, Brazil	3	13	53.33±10.83	0.09±0.04
Tarija Basin (Trj)	Tarija, Bolivia	6	28	77.30±4.92	0.17±0.04
Serengeti (Ser)	N Tanzania	5	16	73.84	0.10
Kruger Park (Kru)	NE South Africa	5	22	61.99	0.07
Mala Mala Reserve (Mal)	NE South Africa	4	18	74.07	0.16

Table 2. Goodness of fit (as measured by the *AIC*) and the expected fraction of predator-prey interactions correctly predicted by each model (f_c) between African large mammals in three sites. Name codes in Table 1.

	PNM		*LRM*	
	AIC	f_c	*AIC*	f_c
Ser	71.4	0.77	72.3	0.74
Kru	90.88	0.76	68.82	0.83
Mal	85.74	0.70	76.32	0.68

Despite the differences in the composition and body size distribution of each Pleistocene community (Fig. 1) their structure was most likely very similar: All networks showed a large absolute degree of nestedness and small degree of modularity (see Table 1). Comparing the relative degrees of nestedness and modularity across assemblages we found the degree of nestedness and modularity of African assemblages are a subset within the range defined by the Pleistocene networks (Fig. 2).

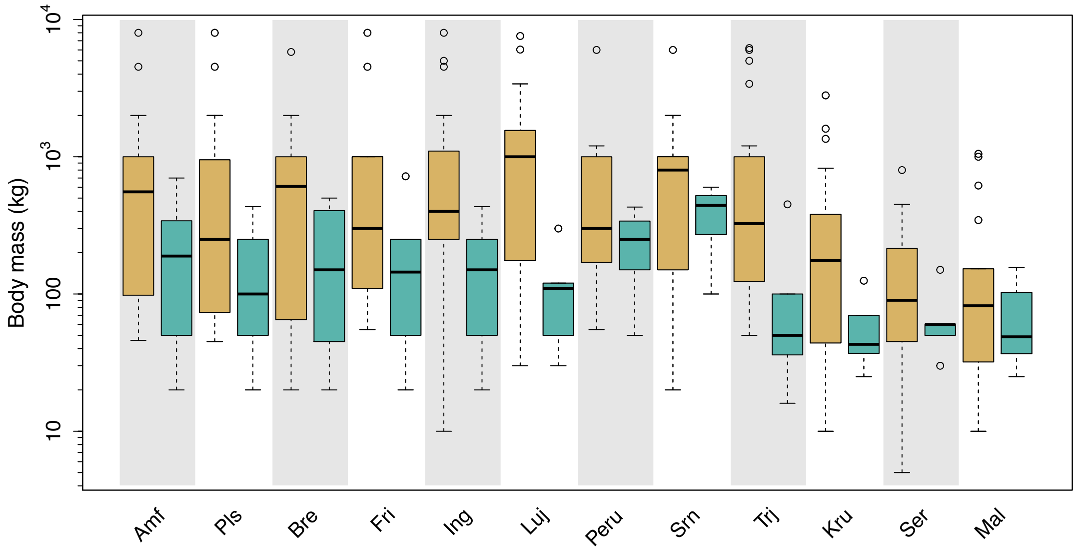

Figure 1. Body size distribution of predators (green) and prey (yellow) for each assemblage. Name codes in Table 1.

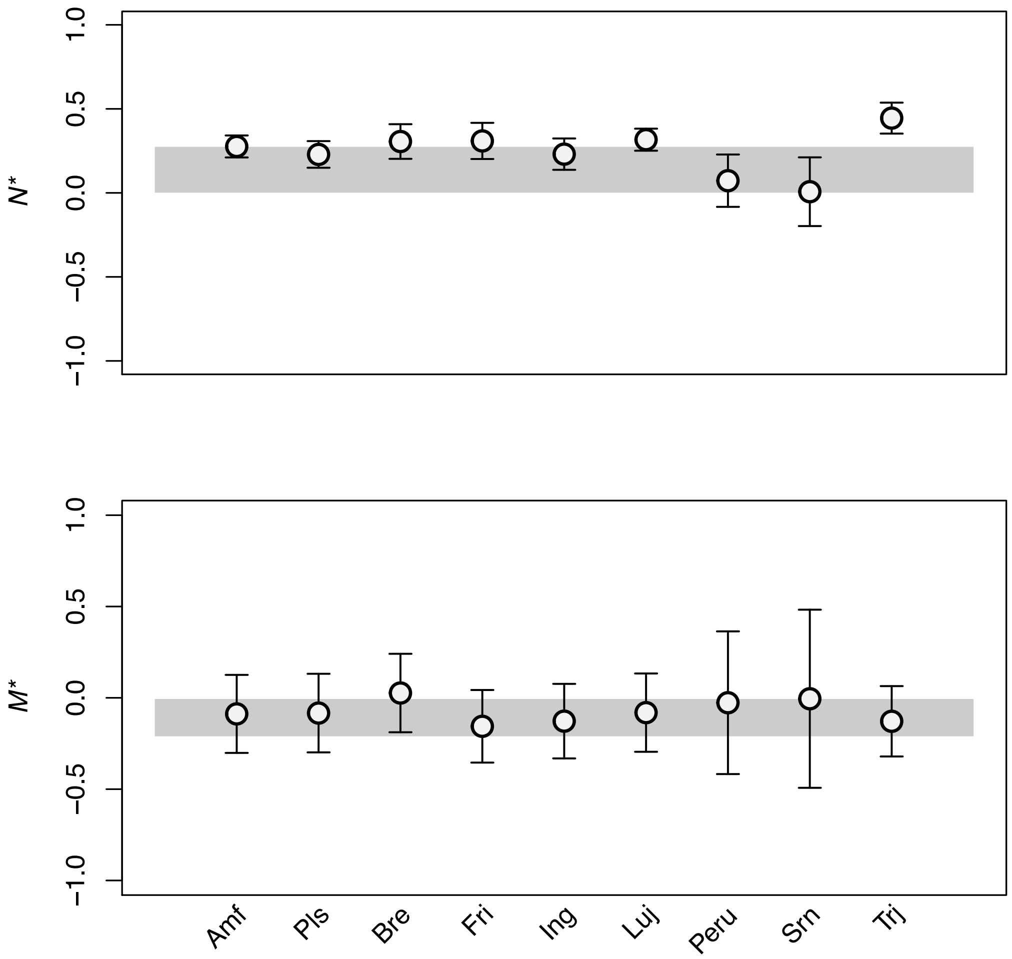

Figure 2. Average relative nestedness (N^*) and modularity (M^*) of Pleistocene predator-prey networks. The shaded area represents the range of N^* and M^* for the three modern African communities. Error bars depict ± SD.

Current large-mammal assemblages in North and South America are largely depauperate in comparison to Pleistocene large-mammal assemblages (Fig. 3). The networks comprising only surviving species are more tightly packed (smaller average shortest path, *D; Fig. 3*) and their structure is more dependent on a small subset of species, mainly predators (larger central point dominance, *CPD*; Fig. 3).

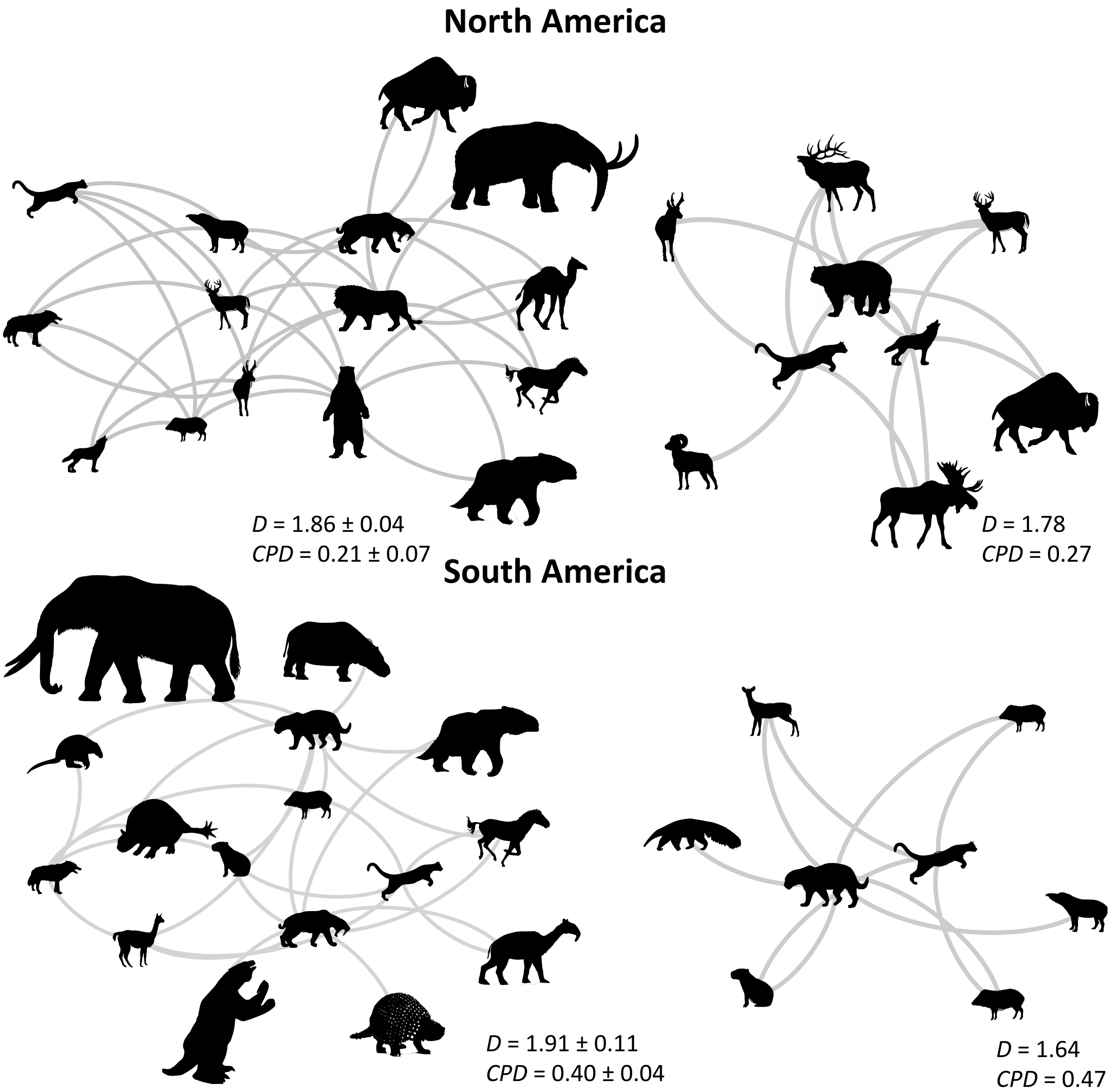

Figure 3. Predator-prey interactions between large mammals in the Pleistocene (left) and at present (right) in North and South America. Pleistocene networks are represented by one potential network reconstructed using the LRM. The large-mammal faunas from La Brea and Yellowstone represent North America. The large-mammal faunas from Luján and the Pantanal region represent South America. Values denote the average shortest path, *D*, and central point dominance, *CPD*, for Pleistocene (average ± SD for 100 potential networks) and modern networks. We aggregated a few species in Pleistocene networks to ease visualization.

DISCUSSION

We showed here network models parameterized with body mass information are able to reproduce much of the interaction patterns among large mammals. Using such network models we reconstructed potential networks of interaction between late Pleistocene mammals in the Americas and showed their structure would have been similar to modern mammal assemblages in Africa, but networks suffered major structural changes after the extinctions.

Previous studies using network models parameterized with body mass information showed body size alone is unable to predict interaction patterns of several species in food webs (Rohr *et al.* 2010; Williams *et al*. 2010). Here we show that when focusing on smaller "subnetworks", with only two trophic levels and fewer groups, the performance of such models is greatly improved. A good fit of models parameterized only with body mass to a whole food web would indicate body size translates into interaction patterns in a similar way for different groups and different trophic levels, which seems unlikely. In contrast, our dataset includes only large mammalian predators, all carnivorans, and prey, mostly ungulates. It is reasonable to assume that this smaller set of species obey similar rules regarding how interaction patterns are mapped into body size relationships. Network models have also been used to test whether ancient networks reconstructed using paleocological inferences share similarities with modern communities (Dunne *et al.* 2008). We feel using network models to reconstruct networks of interaction representing ancient systems is promising and might bring insights on the structure and dynamics of other paleocological systems. In this study, the combination of food web models and paleontological data allowed us to infer the organization of Pleistocene networks and to discuss consequences of this organization for system dynamics.

Modern Africa bears the largest extant terrestrial mammals, but the body-mass distribution of Pleistocene mammals in the Americas was even more skewed towards larger species (Koch & Barnosky 2006). Because the model we used assumes body-mass ratios determine the probability of interactions, such differences in species composition and body-size structure could have resulted in assemblages with different structural patterns. However, we showed here that the overall structure of Pleistocene predator-prey networks in the Americas was most likely similar to what we find today in the African savannas. Pleistocene predator-prey networks were likely highly nested and non-modular, similar to the extant large-mammal communities (Sinclair *et al.* 2003) and contrasting with other types of antagonistic networks (Pires & Guimarães 2013).

Although the overall structure of whole food webs, comprising several trophic levels, often show a high degree of modularity (Baskerville *et al.* 2011), food webs are formed by connected subnetworks that are often nested (Kondoh *et al.* 2010). In fact when the degree of biological association between interaction partners is low antagonistic interactions are expected to form nested networks (Pires & Guimarães 2013). Nestedness means the resource use patterns of consumers overlap asymmetrically, what should have implications for competition and, thus, coexistence (Kondoh *et al.* 2010). Moreover, nestedness is frequently associated with lower stability for networks depicting antagonistic interactions (Thébault & Fontaine 2010; Allesina & Tang 2012). The intrinsic instability of nested networks can be counterweighted by patterns of interaction strength (Staniczenko *et al.* 2013). An open avenue for future work on the structure of Pleistocene systems is to estimate the strength of interactions and evaluate whether different patterns emerge. Based on recent results using isotope analyses (Yeakel *et al.* 2013) we expect that by considering the strength of interactions modularity should increase, what is often related to higher stability, and could help explaining the co-occurrence of so many large species with overlapping interaction patterns.

We showed the interactions of Pleistocene large mammals and modern African large mammals were most likely organized in a similar way. Still, Pleistocene large-mammal assemblages collapsed in the Americas, whereas large-mammal assemblages still persist in Africa. This differential survival may be related to other aspects of the community organization. For example, the larger number of interacting species in Americas provides several potential pathways by which species indirectly affect each other (Forster 2003; Ripple & Van Valkenburgh 2010). Moreover, the large number of slow-breeding animals in Pleistocene assemblages could have made the populations less likely to recover after perturbations (Johnson 2002; Koch & Barnosky 2006). In addition to the climate changes and anthropogenic impacts that might have triggered the extinctions (Koch & Barnosky 2006), the interplay between the nested structure, high species richness and slow breeding might have contributed to the collapse of Pleistocene large-mammal assemblages. The relative contribution of each of these factors remains an open question.

By now we show the Pleistocene extinction not only eroded the diversity of mammalian assemblages but also disrupted the organization of interactions between large mammals. The current large-mammal interaction networks in the Americas are more compact, with all species a few links apart from each other. This arrangement has implications for dynamics as the effects of perturbations are much more likely to spread in smaller networks where all species are closely connected (Williams *et al.* 2002). In addition, current large-mammal assemblages are more dependent on a few species central to network structure. Species rich-systems will often have high levels of functional redundancy and thus the loss of one or a few species may be compensated by the remaining ones. In contrast, species-poor systems such as current large-mammal assemblages, lack functional redundancy and are thus more vulnerable to species loss, which is likely to result in trophic cascades (Terborgh & Estes 2010). A classic example is the sea otter/kelp forest system in which the loss of one single species, the sea otter (*Enhydra lutris*), leads to great changes in the landscape (Estes & Duggins 1995). However, unlike in the sea otter case, the lack of functional redundancy and dependence on a few central predators in terrestrial large-mammal communities (Ripple & Beschta 2003; Estes *et al.* 2011) is most certainly linked to the Pleistocene extinctions. We showed here that large-mammal assemblages were not as centralized and tightly packed in the Pleistocene as they are today. We hypothesize the disruption of large-mammal networks led to the omnipresence of systems that hinge upon a few species central to network structure and dynamics and are thus highly vulnerable to species loss.

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APPENDICES

Appendix S1. Composition of Pleistocene and modern large-mammal assemblages

North America:

La Brea Tar Pits		American Falls Area		Friesenhahn Cave		Ingleside		Page-Ladson Site	
	Body mass (kg)		Body mass (kg)		Body mass (kg)		Body mass (kg)		Body mass (kg)
PROBOSCIDAE		**PROBOSCIDAE**		**PROBOSCIDAE**		**PROBOSCIDAE**		**PROBOSCIDAE**	
Mammut americanum	4523	*Mammuthus columbi*	8000	*Mammuthus columbi*	8000	*Mammuthus columbi*	8000	*Mammuthus columbi*	8000
XENARTHRA		*Mammut americanum*	4523	*Mammut americanum*	4523	*Mammut americanum*	4523	*Mammut americanum*	4523
Nothrotheriops shastensis	600	**XENARTHRA**		**PERISSODACTYLA**		*Cuvieronius* sp.	5000	**XENARTHRA**	
Paramylodon harlani	2000	*Megalonyx jeffersonii*	600	*Equus* sp.	300	**XENARTHRA**		*Megalonyx jeffersonii*	600
PERISSODACTYLA		*Paramylodon harlani*	2000	*Tapirus veroensis*	275	*Megalonyx jeffersonii*	600	*Paramylodon harlani*	2000
Equus occidentalis	615	**PERISSODACTYLA**		**ARTIODACTYLA**		*Paramylodon harlani*	2000	*Glyptotherium floridanum*	1100
Tapirus californicus	200	*Equus scotti*	555	*Bison* sp.	800	*Glyptotherium floridanum*	1100	*Holmesina septentrionalis*	250
ARTIODACTYLA		**ARTIODACTYLA**		*Odocoileus virginianus*	55	*Holmesina septentrionalis*	250	*Dasypus bellus*	45
Bison antiquus	1000	*Bootherium bombifrons*	300	*Mylohyus fossilis*	67	**PERISSODACTYLA**		**PERISSODACTYLA**	
Bison occidentalis	900	*Bison alaskensis*	800	*Platygonus compressus*	110	*Equus complicatus*	400	*Equus* sp.	300
Odocoileus hemionus	80	*Bison latifrons*	900	*Camelops* sp.	1000	*Equus pacificus*	300	*Tapirus veroensis*	250
Antilocapra americana	50	*Cervus elaphus*	156	**CARNIVORA**		*Equus fraternus*	259	**ARTIODACTYLA**	
Capromeryx minor	20	*Odocoileus* sp.	55	*Smilodon fatalis*	250	*Tapirus veroensis*	275	*Bison antiquus*	800
Camelops hesternus	1000	*Rangifer tarandus*	86	*Homotherium serum*	189	**ARTIODACTYLA**		*Odocoileus virginianus*	55
Platygonus sp.	20	*Antilocapara americana*	46	*Panthera onca augusta*	100	*Bison antiquus*	800	*Mylohyus fossilis*	67
CARNIVORA		*Platygonus* sp.	50	*Lynx rufus*	20	*Odocoileus virginianus*	55	*Platygonus vetus*	50
Smilodon fatalis	250	*Camelops hesternus*	1000	*Arctodus simus*	500	*Capromeryx minor*	20	*Palaeolama mirifica*	80
Panthera leo atrox	430	*Hemiauchenia macrocephala*	110	*Canis dirus*	50	*Platygonus compressus*	110	*Hemiauchenia macrocephala*	110
Puma concolor	50	**CARNIVORA**				*Palaeolama mirifica*	80	**CARNIVORA**	
Lynx rufus	20	*Smilodon fatalis*	250			*Camelops* sp.	1000	*Smilodon fatalis*	250
Ursus arctos	380	*Homotherium serum*	189			**CARNIVORA**		*Panthera leo atrox*	433
Arctodus simus	500	*Panthera leo atrox*	433			*Smilodon fatalis*	250	*Panthera onca*	100
Canis dirus	50	*Puma concolor*	50			*Panthera leo atrox*	433	*Lynx rufus*	20

Canis lupus	40	*Lynx canadensis*	20	*Lynx rufus*	20	*Canis dirus*	50
		Arctodus simus	700	*Tremarctus floridanus*	150		
		Canis dirus	50	*Canis dirus*	50		

South America:

Guerrero Member – Luján		Tarija Basin		São Raimundo Nonato		Talara Tar Seeps	
	Body mass (kg)		Body mass (kg)		Body mass (kg)		Body mass (kg)
PROBOSCIDAE		**PROBOSCIDAE**		**PROBOSCIDAE**		**PROBOSCIDAE**	
Stegomastodon platensis	7580	*Haplomastodon* sp.	6000	*Haplomastodon chimborazi*	6000	*Haplomastodon* sp.	6000
XENARTHRA		*Cuvieronius tropicus*	5000	**XENARTHRA**		**XENARTHRA**	
Megatherium americanum	6037	*Notiomastodon* sp.	6193	*Eremotherium laurillardi*	800	*Eremotherium* sp.	800
Lestodon australis	3397	**XENARTHRA**		*Scelidodon* sp.	1000	*Scelidotherium* sp.	1000
Glossotherium robustum	1713	*Nothropus tarijensis*	100	*Catonyx cuvieri*	500	*Glossotherium* sp.	1200
Scelidotherium leptocephalum	1057	*Scelidodon tarijensis*	1000	*Glyptodon clavipes*	2000	*Pampatherium* sp.	170
Panochthus tuberculatus	1100	*Lestodon armatus*	3397	*Pampatherium humboldtii*	150	**PERISSODACTYLA**	
Doedicurus clavicaudatus	1468	*Glossotherium tarijensis*	1200	**NOTOUNGULATA**		*Equus* sp.	300
Glyptodon clavipes	2000	*Hoplophorus echazui*	280	*Toxodon* sp.	1000	*Tapirus* sp.	250
Glyptodon reticulatus	862	*Panochthus tuberculatus*	1061	**LITOPTERNA**		**ARTIODACTYLA**	
Neothoracophorus depressus	1100	*Neothoracophorus elevatus*	800	*Macrauchenia patagonica*	988	*Odocoileus* sp.	55
Plaxaplous canaliculatus	1300	*Glyptodon reticulatus*	862	**PERISSODACTYLA**		**RODENTIA**	
Pampatherium typum	200	*Chlamydotherium sellowi*	175	*Hippidion bonaerensis*	200	*Neochoerus* sp.	70
Eutatus seguini	200	*Pampatherium humboldtii*	150	**ARTIODACTYLA**		**CARNIVORA**	
NOTOUNGULATA		**NOTOUNGULATA**		*Mazama* sp.	20	*Smilodon fatalis*	250
Toxodon platensis	1000	*Toxodon platensis*	1000	*Pecari tajacu*	32	*Panthera leo atrox*	430
LITOPTERNA		**LITOPTERNA**		*Tayassu pecari*	21	*Canis dirus*	50
Macrauchenia patagonica	988	*Macrauchenia patagonica*	988	*Palaeolama major*	1000		
PERISSODACTYLA		**PERISSODACTYLA**		**CARNIVORA**			
Equus neogeus	300	*Onohippidium devillei*	300	*Arctotherium brasiliense*	600		
ARTIODACTYLA		*Hippidion bonaerensis*	250	*Panthera onca*	100		
Morenelaphus lujanensis	50	*Hippidion principale*	511	*Smilodon populator*	442		
Tayassu tajacu	30	*Equus insulatus*	351				
Eulamaops paralellus	150	*Tapirus tarijensis*	200				
Lama guanicoe	90	**ARTIODACTYLA**					
Lama gracilis	50	*Charitoceros tarijensis*	60				
Hemiauchenia paradoxa	1000	*Hippocamelus* sp.	68				

RODENTIA		*Lama oweni*	100
Neochoerus aesopi	63	*Lama provicugna*	50
CARNIVORA		*Lama glama*	147
Smilodon populator	300	*Palaeolama* sp.	1000
Panthera onca	100	**RODENTIA**	
Puma concolor	50	*Neochoerus* sp.	70
Arctotherium sp.	110	*Hydrochoerus* sp.	62
Dusicyon avus	30	**CARNIVORA**	
		Smilodon populator	450
		Panthera onca	100
		Puma concolor	50
		Canis dirus	50
		Theriodictis tarijensis	36
		Protocyon troglodites	16

Africa:

Serengeti National Park		Kruger National Park		Mala Mala Reserve	
	Body mass (kg)		Body mass (kg)		Body mass (kg)
PERISSODACTYLA		**PROBOSCIDAE**		**PERISSODACTYLA**	
Equus quagga	250	*Loxodonta africana*	2800	*Ceratotherium simum*	1050
ARTIODACTYLA		**PERISSODACTYLA**		*Equus quagga*	152
Giraffa camelopardalis	800	*Ceratotherium simum*	1600	**ARTIODACTYLA**	
Syncerus caffer	450	*Equus quagga*	310	*Hippopotamus amphibius*	1000
Taurotragus oryx	400	**ARTIODACTYLA**		*Giraffa camelopardalis*	617
Kobus ellipsiprymnus	180	*Hippopotamus amphibius*	1350	*Syncerus caffer*	345
Connochaetes taurinus	170	*Giraffa camelopardalis*	825	*Tragelaphus strepsiceros*	136
Alcelaphus buselaphus	150	*Syncerus caffer*	520	*Kobus ellipsiprymnus*	132
Damaliscus lunatus	120	*Taurotragus oryx*	380	*Damaliscus lunatus*	110
Phacochoerus africanus	60	*Hippotragus equinus*	260	*Connochaetes taurinus*	110
Redunca arundinum	60	*Hippotragus niger*	220	*Tragelaphus angasii*	54
Aepyceros melampus	50	*Connochaetes taurinus*	220	*Potamochoerus porcus*	45
Nanger granti	50	*Kobus ellipsiprymnus*	180	*Phacochoerus africanus*	38
Tragelaphus scriptus	40	*Tragelaphus strepsiceros*	170	*Tragelaphus scriptus*	38
Eudorcas thomsoni	20	*Damaliscus lunatus*	127	*Aepyceros melampus*	32
Ourebia ourebi	18	*Tragelaphus angasii*	63	*Redunca arundinum*	32
Madoqua kirkii	5	*Phacochoerus africanus*	58	*Sylvicapra grimmia*	15
CARNIVORA		*Redunca arundinum*	45	*Oreotragus oreotragus*	10
Panthera leo	150	*Aepyceros melampus*	44	*Raphicerus campestris*	10
Panthera pardus	60	*Tragelaphus scriptus*	40	**CARNIVORA**	
Crocuta crocuta	60	*Sylvicapra grimmia*	17	*Panthera leo*	156
Acinonyx jubatus	50	*Oreotragus oreotragus*	13	*Panthera pardus*	49
Lycaon pictus	30	*Raphicerus campestris*	11	*Acinonyx jubatus*	48
		Raphicerus sharpei	10	*Lycaon pictus*	25
		CARNIVORA			
		Panthera leo	125		
		Crocuta crocuta	70		
		Lycaon pictus	25		
		Panthera pardus	37		
		Acinonyx jubatus	43		

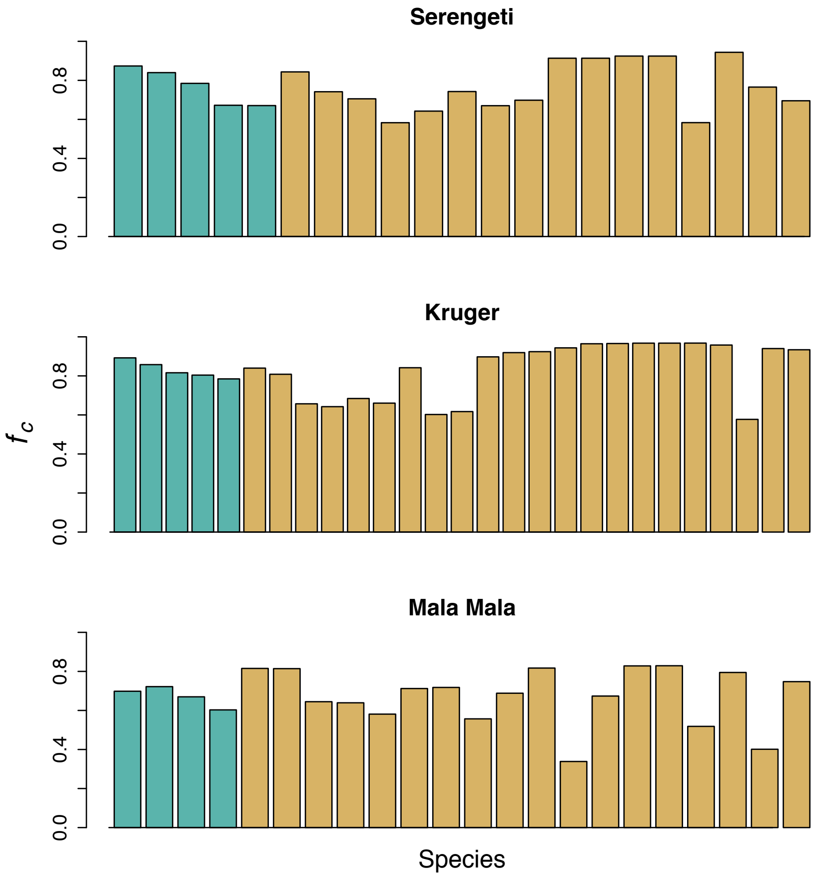

Fig S1. Fraction of presences and absences of pairwise interactions (f_c) correctly predicted by the LRM for each species in each network representing African assemblages. Green bars represent predators and yellow bars prey species.

CAPÍTULO 4

THE NETWORK ORGANIZATION OF MEGAFAUNA ASSEMBLAGES MADE THEN VULNERABLE TO HUMAN ARRIVAL

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Abstract. The end of the Pleistocene was marked by the extinction of almost all large land mammals (the megafauna) everywhere except in Africa. The debate on the megafaunal extinction has focused on possible external triggers for the event, such as climate change and direct and indirect effects of humans. However, the impact of such triggers depends on the organization of species interactions, which modulates how perturbations propagate. We combined network models, extinction simulations, and data on extinct and extant megafaunal assemblages to investigate if differences in the organization of Pleistocene and modern communities explain why the megafauna died out in the Americas while persisting in Africa. We show that Pleistocene communities should not have been more responsive to small perturbations than extant African communities, but differences in the features that determine the organization of species interactions, such as species richness and body-size distributions, made Pleistocene communities remarkably more vulnerable to the arrival of new predators such as humans. Our findings show that extinction events have to be addressed taking into account not only the effects of external processes but also information on the network organization of species assemblages, which can contribute to our understanding of past and future large extinction events.

INTRODUCTION

The end of the Pleistocene was marked by an extinction event (the Late Quaternary Extinction, LQE) that led to the demise of large vertebrates, profoundly affecting the organization of ecosystems worldwide (Martin & Klein 1984; Koch & Barnosky 2006). The greatest impact was on the mammalian megafauna (body mass ≥ 44 kg) with the extinction of more than 100 genera (Koch & Barnosky 2006; Barnosky 2008). The LQE was particularly severe in Australia and the Americas where more than 70% of the megafauna genera perished (Koch & Barnosky 2006). Africa retains the remnants of these once widespread megafauna assemblages (including species weighing > 1,000 kg; Owen-Smith 1987). Studies on the causes of the LQE focus mostly on potential external triggers for the extinctions (Scott 2010), such as direct (Martin & Klein 1984; Alroy 2001) and indirect (Barnosky *et al.* 2004; Koch & Barnosky 2006) impacts of humans, climate change (Guthrie 1984), and combinations of these factors (Barnosky 2008; Prescott *et al.* 2012). However, extinctions result not only from external factors that disturb ecosystems (Newman & Palmer 2002). Community organization, as determined by species interactions, dictates how perturbations affect the community (Forster 2003; Roopnarine 2006). Therefore, the answer for why large mammals died out almost everywhere except Africa could reside not only in the perturbations themselves, but, at least in part, in the interactions within megafauna assemblages.

Theory shows that basic features of ecological systems have large effects on the way perturbations propagate (Rooney & McCann 2012). Specifically, species richness, the number and strength of interactions, and the way such interactions are organized determine the probability that population densities within a community will reestablish (stability) or diverge (instability) after a perturbation (May 1972; Neutel *et* *al.* 2007; Allesina & Tang 2012). If communities are unstable or populations take too long to reestablish*,* fluctuations may reduce populations to low densities, making them vulnerable to demographic stochasticity and ultimately local extinction.

Here we combine paleontological and ecological data, extinctions simulations, and network theory, which deals with the organization and dynamics of interactive systems, to explore the role of species interactions in shaping the dynamics of past and present assemblages of large mammals. First, we investigate whether differences in the organization of Pleistocene and surviving African large-mammal communities offer insights on why the former collapsed while the later persisted. Then we evaluate if the basic characteristics of large-mammals communities can explain extinction patterns in the Late Pleistocene in Americas. Finally, to understand possible effects of the arrival of humans to the Americas, we test how the invasion by a new predator would impact the dynamics in different locations by altering community organization.

METHODS

Large-mammal assemblages

We searched the literature and the Paleobiology Database (http://paleodb.org/) for Pleistocene fossil assemblages for which the composition, chronology, and taphonomy suggest an actual community of interacting species. We avoided sites with a mammalian fauna that seemed incomplete based on our general knowledge of Pleistocene faunas or those with dates that were too unconstrained, which might have yielded time-averaged assemblages. We ended up with five Late Pleistocene sites in North America and four sites in South America (Table S1 in Appendices). For the comparison with modern systems we used mammalian assemblages from three localities in Africa (see Table S1 in Appendices). We considered only the large-mammal assemblages within communities, which form compartments loosely connected, both structurally and dynamically, with the rest of the food web (Terborgh & Estes 2010). Because we are interested in interactions among large mammals, we established systematic criteria to determine which species to consider. We considered only mammalian herbivores larger than 5 kg, which are more likely to be preyed upon by the carnivores that make up the large mode of the body-size distribution (Carbone *et al.* 1999; Owen-Smith & Mills 2008). Accordingly, we only included carnivore species with body mass greater than 20 kg that had evidence of hypercarnivory. In this way we avoided including carnivores such as small felids, which rely mainly on rodents or other small prey, or large omnivores, such as some bears (Carbone *et al.* 1999; Figueirido & Soibelzon 2010), both of which probably played a minor role in the predator-prey dynamics of large-mammal assemblages. We obtained data on the body mass of Pleistocene mammals from compiled data available in the literature (Smith *et al.* 2003). When no body mass estimate was available for a given species, we used the average body mass of species within the same genus.

Reconstructing predator-prey interaction networks

Despite the insights brought by indirect evidence of interactions (Marean & Ehrhardt 1995) and isotope analysis (Yeakel *et al.* 2013), determining who interacted with whom in paleocological systems is challenging (Roopnarine 2006; Dunne *et al.* 2008). To account for the uncertainty inherent to any characterization of ecological networks we used a probabilistic model (Rohr *et al.* 2010) to generate ensembles of possible Pleistocene networks with a realistic structure. Because body size has a central role in structuring African large-mammal communities (Sinclair *et al.* 2003; Owen-Smith & Mills 2008), and ecological networks in general (Woodward *et al.*

2005), we parameterized the model using the body mass of herbivores and predators (Fig. 1).

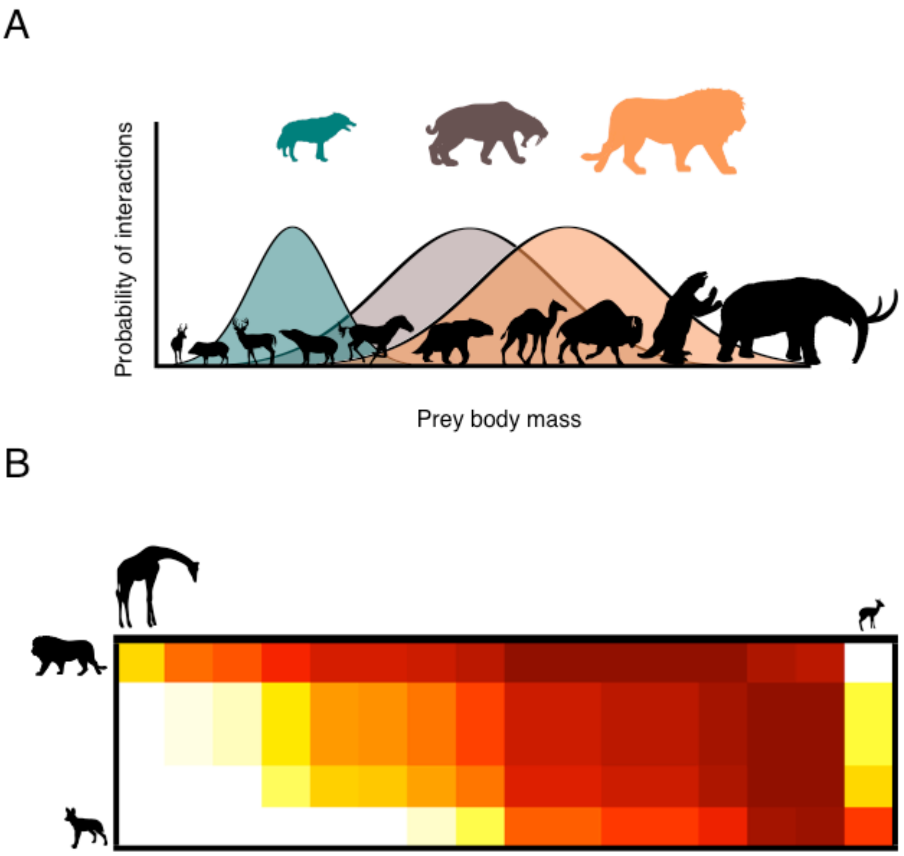

Figure 1. Reconstructing predator-prey interactions. **A**) Conceptual representation of the model used to reconstruct predator-prey interaction networks. The model assumes body-mass relationships determine the probability of interactions between predators and prey, as depicted by the probability curves corresponding to each predator. **B**) Example of a probability matrix produced by a model run parameterized with the information for a system from Africa. The color heat illustrates the probability of each interaction between predators (rows) and prey (columns). This model correctly reproduced on average 75% of the interactions within the three predator-prey systems from modern Africa[1].

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[1] Capítulo 3 - The disruption of predator-prey interaction networks after megafaunal extinctions

In this model the probability of an interaction between predator *i* and prey *j* is a function of the log ratio of the body mass (*m*) of *i* over the body mass of *j* (Brose *et al.* 2006) and can be represented as a logit regression of the form:

$$\log\left[\frac{P(a_{ij}=1)}{P(a_{ij}=0)}\right] = \alpha + \beta\log\left(\frac{m_i}{m_j}\right) + \gamma\log^2\left(\frac{m_i}{m_j}\right) \tag{1}$$

in which a_{ij} is a cell in the binary matrix **A** that depicts species interactions and α, β, *and* γ are parameters to be estimated. The model has a quadratic polynomial term and, hence, the interaction probabilities form a Gaussian-like curve reflecting the idea of an optimal range for the predator. This formulation is consistent with other food-web models based on the niche concept (Williams & Purves 2011). Thus, the probability of an interaction between predator *i* and prey *j* given a particular parameter set $\theta = \{\alpha, \beta, \gamma\}$ is:

$$P(i,j \mid \theta) = \frac{e^{\alpha+\beta\log\left(\frac{m_i}{m_j}\right)+\gamma\log^2\left(\frac{m_i}{m_j}\right)}}{1+e^{\alpha+\beta\log\left(\frac{m_i}{m_j}\right)+\gamma\log^2\left(\frac{m_i}{m_j}\right)}} \tag{2}$$

To test the performance of the model in reproducing predator-prey interactions among large mammals we used the three sites in Africa for which we had actual data on predator-prey interactions (Table S1). First, we used a logit regression to find the maximum likelihood estimates (MLE) of parameters α, β, and γ for each location. Then, we used the MLE and equation 2 to generate a matrix **P** in which each cell, $p_{i,j}$, described the probability of interaction between predator *i* and prey *j.* The probability matrix **P** allows computing the expected number of cells a_{ij} in matrix **A** correctly predicted by the model:

$$N_c(\mathbf{A} \mid \theta) = \sum_i\sum_j a_{ij}P(i,j \mid \theta) + \sum_i\sum_j (1-a_{ij})(1-P(i,j \mid \theta)) \tag{3}$$

The expected fraction of cells predicted correctly, f_c, is obtained by dividing N_c by the number of cells in **A** (Williams & Purves 2011). The model performed well in reproducing the three networks representing large-mammal interactions in Africa[2] (f_c = 83%, 68% and 74%; Ser, Mal, and Kru, respectively; see Table 1 for acronyms), indicating that it is able to generate realistic structures of predator-prey interactions.

Given this result, we used the same model to generate predator-prey networks among the Pleistocene mammals at each site. To do so, we first defined the range of the three parameters α, β, and γ. The extremes of the range of each parameter were the smallest and largest values found as MLEs for the three African sites. By doing so, we adopt the assumption that the constraints imposed on diet by the body-mass relationship between predator and prey were similar in Pleistocene and modern African large-mammal communities (Prevosti & Vizcaíno 2006). Although we used the parameters estimated for the African networks, the parameters only determine how the probability of interactions are linked to body mass relationships. The number of predator and prey species and body mass distribution in each assemblage are the factors that determine the network organization.

To generate a predator-prey network we then sampled values of α, β, and γ within the defined range and computed all p_{ij} to obtain a matrix **P**. The matrix **P** was then used to generate a potential binary matrix, **A**, depicting interactions among predator and prey species in each assemblage. Because this procedure envisages incorporating the uncertainty inherent to inferring interactions among extinct species, we generated 1000 possible interaction networks for each site.

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[2] Capítulo 3 - The disruption of predator-prey interaction networks after megafaunal extinctions

The community matrix

To analyze the dynamical behavior of these potential interacting assemblages each binary matrix **A** was transformed in an adjacency matrix **Q** of size $S \times S$, being S the total number of species, in which a cell, q_{ij}, represents the effect of species i on species j (interaction strength) around a feasible equilibrium (Allesina & Tang 2012). Thus **Q** can be viewed as an approximation to the Jacobian matrix (Allesina & Tang 2012). To build **Q** all diagonal elements, representing the effect of intraspecific interactions, were assigned -1. Off-diagonal elements q_{ij} were only $\neq 0$ if $a_{ij} = 1$.

We used different methods to assign values to off-diagonal coefficients. The first method is similar to previous work on the stability of food webs (Allesina & Tang 2012). Each cell $q_{ij} \neq 0$ was assigned a value x_{ij} drawn from a normal distribution with parameters $\mu = 1$ and $\sigma = 1$. Because prey have positive effects on the demography of predators, but predators have negative effects on prey populations, we used $-|x_{ij}|$ when q_{ij} represented the effect of predator i on prey j and $|x_{ji}|$ for the effect of prey j on predator i. Note that $q_{ij} \neq q_{ji}$. We chose a Gaussian distribution centered around 1 because it guarantees that most of the values representing interaction strengths will be small while only a few will be large, a pattern that is often found in nature (Wootton & Emmerson 2005). Moreover, the parameters used avoid situations such as matrices with very low interaction strengths, in which the effect of intraspecific competition (set to 1) is much larger than that of interspecific interactions. Although assuming strong intraspecific competition leads to stable dynamics (Allesina & Tang 2012), a higher role of intraspecific competition for all species in the predator-prey assemblage is very unlikely (Owen-Smith & Mills 2008). Conversely, if the mean interaction strength were too large the effects of intraspecific interactions become negligible for all species, inducing unstable behavior in all matrices. Again this is an unlikely scenario in predator-prey assemblages (Owen-Smith & Mills 2008). Therefore, by choosing an intermediate value, we simulate a more plausible scenario. Similar to the results of Allesina and Tang (2012) on the consequences of using different distributions for interaction strengths, exploratory analyses where we varied the distribution of interaction strengths showed that different distributions yield results that are qualitatively similar (results not shown). To compute confidence intervals we repeated analyses 100 times for each site.

The dynamics of the potential communities under a small perturbation are given by the real part of the leading eigenvalue, $Re\lambda$, of **Q** (May 1972; Allesina & Tang 2012). We computed the proportion of matrices with stable behavior, $Re\lambda < 0$, as a measure of the probability that communities are stable, P_{st}. For matrices presenting stable behavior we also computed the average time to return to equilibrium, $\tau \sim 1/|Re\lambda|$ (Loeuille 2010).

Asymmetry in the distribution of interaction strengths

The efficiency of predators in converting prey into actual population growth is unlikely to be close to maximum. Thus the per capita effect of the prey on the predator may be smaller than the converse. Several studies on food web dynamics have considered this asymmetry in interaction strengths (Pimm & Lawton 1978; Emmerson & Yearsley 2004). To test the effect of breaking the symmetry between the distributions of interaction strengths we reran all tests assuming the average per capita effects of predators upon their prey are twice as large as the effect of prey on predators. We did this by drawing interaction strengths from different distributions ($\mu_1 = \mu_2/2$). Breaking the symmetry in interaction strength distributions did not alter the results qualitatively (Tables S2 to S5 in Appendices).

Interaction strength as a function of body mass

If we assume the body-size relationship between predator and prey determines the probability of interactions, it may affect the demographic effect of interactions as well (Woodward *et al.* 2005; Brose *et al.* 2008). Therefore we tested the effects of assigning interaction strengths in matrix **Q** as a function of body-size relationships by defining the off-diagonal elements as:

$$q_{ij} = a_{ij} y_{ij} e^{-\left(m_i - m_j\right)^2} \qquad (4),$$

where the term y is a random value drawn from a normal distribution with parameters $\mu = 1$ and $\sigma = 1$. This formulation was adapted from studies on coevolution that model the outcome of species interactions taking into account phenotype matching (Nuismer *et al.* 2010; Yoder & Nuismer 2010). Such a formulation implies smaller interaction effects for species that differ in size by a great amount. The random variable adds noise to the relationship and portrays the uncertainty about how exactly body-mass relationships translate into interaction strengths. By considering the uncertainty of the relationship between body mass and interaction effects, we loosen the constraints imposed by body size. In this way we allow, for instance, that large prey eventually benefits relatively smaller predators, as would be expected for species that also feed on carcasses (Houston 1979) or social predators, such as lions and wolves, which are able to prey upon larger prey (Macdonald 1983).

Assigning interactions effects as a function of body-mass relationships reproduces structural patterns that are more realistic for large-mammal assemblages: large-sized predators will have a stronger impact on populations of medium–sized prey, smaller predators will have larger effects on small prey, and the largest prey are controlled mainly by bottom-up effects (Owen-Smith & Mills 2008). It also increases compartmentalization since predators will tend to interact more heavily with prey within a certain size range (Yeakel *et al.* 2012). Although changing the way we assign interaction strength influences the magnitude of P_{st} and τ, it does not alter the results qualitatively (Tables S2 to S5 in Appendices).

General linear models

To evaluate which components determining community structure are the most important in determining the dynamic behavior of the predator-prey systems we used regression models of the form:

$$P_{st} = \beta_0 + \beta_1 \times R_{pred} + \beta_2 \times R_{pred} + \beta_3 \times M_{pred} + \beta_4 \times M_{prey} \qquad (5),$$

where R_{pred} and R_{prey} are the richness of predator and prey species and M_{pred} and M_{prey} are the average body mass of predators and prey species. We also used a similar model to test how each factor affected τ. All models passed diagnostic tests, performed using R, to check whether the assumptions of general linear tests such as homogeneity of variances and normality of errors applied for each model. We used the Akaike information criterion to select among models including different combinations of explanatory variables. In Tables S4 and S5 (Appendices), for the models with best relative goodness of fit (lowest AIC value), we report the results of the regression analyses for P_{st} and τ for each different method used to assign interaction strengths.

Testing the reliability of P_{st} estimates

It is unlikely that dynamical systems like assemblages of interacting species have only one feasible equilibrium point (Allesina & Tang 2012). Because we built one community matrix **Q** from each interaction matrix **A** generated using the body-mass parameterized model, in the baseline simulations we are analyzing only one of the possible equilibrium points of each system. To test whether this approach would impact the patterns we found, we generated 100 possible matrices **Q** using each of 100 matrices **A** as a template in a total of 10,000 **Q** matrices. We then looked at the real part of the leading eigenvalue of each of the 100 **Q** matrices generated from **A** to determine the probability of stability, P_{st}, of **A.** By doing this we explored distinct possible equilibrium points for each possible structure. We then checked whether the averaged P_{st} over the 100 **A** matrices differed from the P_{st} computed by considering only one equilibrium point for each matrix **A**. As seen in Table S6, these two approaches yield very similar results.

Removal simulations

Unstable communities are not necessarily destined to collapse. A system may reach other equilibrium points with different stability properties after rearranging. To find how changes in the species composition of a given site would impact community dynamics we performed simulations removing species and recalculating the eigenvalues for the resulting community matrices. Starting from 100 community matrices per site we removed species combined in groups of size k ($1 \leq k \leq S - 1$) and registered the change in $Re\lambda$. When the number of combinations for a given k exceeded 10^5 we tested 10^5 random combinations, otherwise we tested all possible combinations of species. We then registered the smallest change in species richness that resulted in the largest reduction in $Re\lambda$ relative to the original matrix. By doing this we searched for assemblages that were stable, highly resilient, but retained a large number of species. We also registered the species composition that yielded the smallest $Re\lambda$ possible. The results of both analyses are reported in Figs S1 and S2 (Appendices).

The effect of humans

The arrival of humans can be seen as the invasion of a new predator that changes community structure. We tested the relative impact of humans by measuring how the addition of a new predator would affect P_{st}. Because in our approach body mass determines interaction patterns, we simulated humans assuming their interaction patterns would be similar to those of large-sized predators (350 kg in our dataset). The effects of humans may be due to their ability to feed on prey of different sizes or just because the networks are vulnerable to the addition of any predator. Because we know adding a predator should, by itself, affect the probability of stability, we estimated the destabilizing effects of humans as the difference in P_{st} after adding humans when compared to the sole effect of adding a predator. To control for the effect adding a predator could have on stability, we measured the effect of adding a small-sized predator (30 kg). We computed the effects of humans on stability as: $(P''_{st,humans} - P'_{st})/P'_{st} - (P''_{st\_control} - P'_{st})/P'_{st}$, where P''_{st} and P'_{st} are the probabilities of stability after and before the additions.

RESULTS

Pleistocene communities were as prone to be unstable as modern African communities. The probability of a community being stable, P_{st}, was not higher and the average time required for stable communities to return to equilibrium, τ, was not lower for the three modern African communities when compared to Pleistocene communities (Table 1). Multiple regression analyses showed both P_{st} ($F_{3,8} = 65.43$; R^2

= 0.94; $p < 0.001$) and τ ($F_{3,8} = 95.76$; $R^2 = 0.96$; $p < 0.001$) were well predicted by basic characteristics of each assemblage (Table S2). Lower P_{st} (Fig. 2) and higher τ were mainly associated with larger predator-richness and lower average prey mass (Table S3). Results hold if matrices are built under different assumptions such as random interaction strengths or body-mass driven interaction strength (Tables S2 to S5).

Table 1. Dynamics of mammalian communities. Probability of stability (P_{st}) and average time (τ) to return to equilibrium of community matrices built for each large-mammal assemblage. Confidence intervals within parentheses. Acronyms are shown after the name for each locality.

	P_{st}	τ
N. America (Pleistocene)		
La Brea Tar Pits (Bre)	0.32 (0.29-0.35)	4.18 (3.84-4.59)
American Falls Area (AmF)	0.30 (0.27-0.33)	3.87 (3.54-4.27)
Friesenhan Cave (Fri)	0.56 (0.53-0.59)	2.86 (2.71-3.03)
Ingleside (Ing)	0.65 (0.62-0.68)	2.06 (1.97-2.16)
Page-Ladson Site (PLS)	0.56 (0.53-0.59)	2.29 (2.19-2.41)
S. America (Pleistocene)		
Guerrero Member – Luján (Luj)	0.71 (0.68-0.74)	1.91 (1.83-1.99)
Tarija (Tar)	0.53 (0.50-0.56)	2.56 (2.34-2.71)
São Raimundo Nonato (SRN)	0.85 (0.82-0.88)	1.25 (1.21-1.29)
Talara Tar Seeps (Tal)	0.85 (0.83-0.87)	1.30 (1.27-1.34)
Africa (Modern)		
Serengeti National Park (Ser)	0.41 (0.38-0.44)	2.56 (2.41-2.73)
Kruger National Park (Kru)	0.47 (0.43-0.50)	2.37 (2.24-2.51)
Mala Mala Reserve (Mal)	0.60 (0.57-0.63)	1.79 (1.72-1.86)

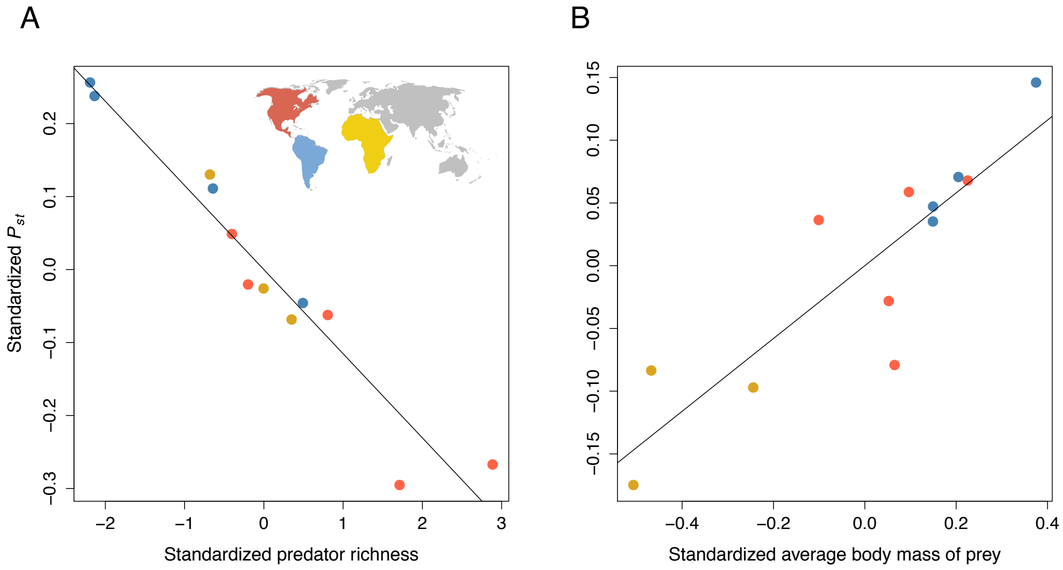

Figure 2. The effect of community structure on stability. Partial regression plots showing the probability of stability of communities, P_{st}, as a function of predator richness (**A**) and the average body mass of prey (**B**) after controlling for all other variables. Different colors represent assemblages from different continents. Values for the y and x axes were standardized by removing the effects of the other variables in the regression model. Test statistics in Table S4.

Simulating extinctions and looking at the dynamics of the resulting communities, we found that communities with fewer predators were more likely to be stable and have smaller τ (Fig. S1). Yet, for all sites (including African), stable communities with the smallest τ are simplified assemblages, with less than 10 large mammals, similar to present-day large-mammal assemblages in the Americas (Fig. S2).

Simulations to test the potential effects of humans showed that the assemblages with an additional large predator, capable of preying upon a wide range of prey, were invariably more prone to instability and had longer return times than original communities, as expected from our results on the destabilizing effects of predators.

Yet, the arrival of humans would affect modern and past communities in distinct ways. In the three modern communities, the effects of humans on the probability of stability would not be greater than the expected effect of adding a smaller predator (Fig. 3). Conversely, in Pleistocene communities, the destabilizing effect of humans would considerably larger (Fig. 3).

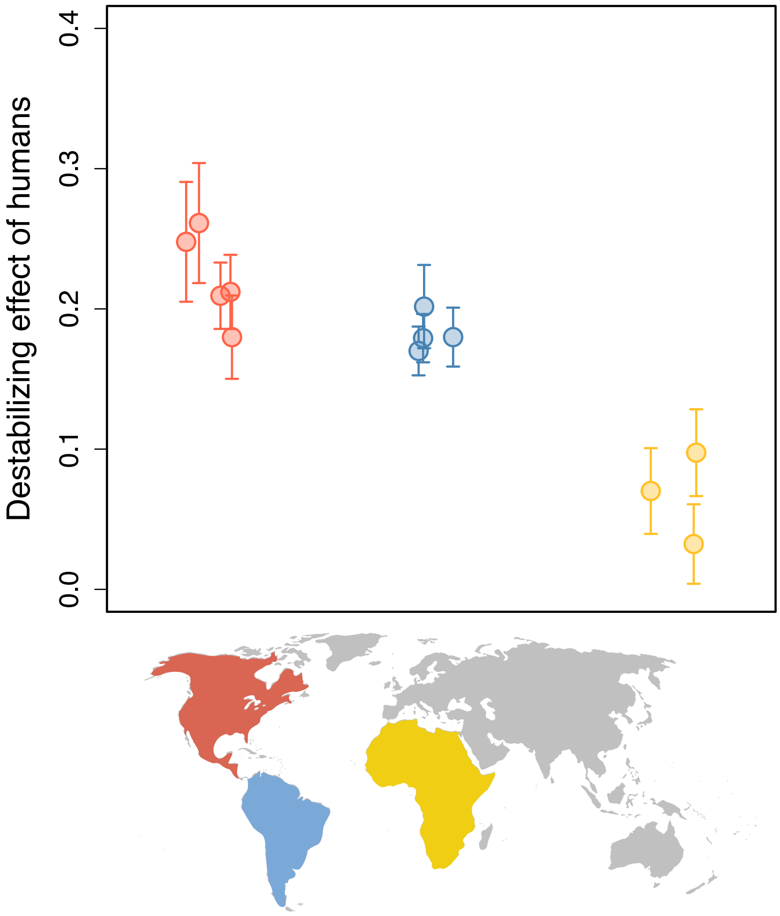

Figure 3. The impact of human arrival on community stability. Each point shows the average (± SD; 100 simulations) destabilizing effect of humans in a given site. Different colors represent assemblages from different continents. Values close to zero mean the destabilizing effect of humans would not be greater than the expected effect of an additional small-sized predator.

DISCUSSION

Our results suggest Pleistocene large-mammal assemblages were not intrinsically prone to be unstable when compared to modern African communities, but were remarkably sensitive to the arrival of a large predator such as humans. Large predators often have large dietary breadths and interact strongly with many species (Sinclair *et al.* 2003; Owen-Smith & Mills 2008). In contrast, large herbivores escape predation from most predators, interacting weakly only with the largest predators (Sinclair *et al.* 2003), and are controlled mainly by bottom-up processes (Owen-Smith & Mills 2008). As a consequence, large predators and large prey have opposite roles in community structure – large predators contribute to increase the connectivity and average interaction strength whereas large prey species contribute to a less connected community with weak interactions. All else being equal, increased connectivity and strong interactions reduce the stability of ecological communities (May 1972; Allesina & Tang 2012; Rooney & McCann 2012). Therefore, the likelihood a perturbation will spread throughout the community should be greater in a community with several large predators, but smaller in communities with many large herbivores.

Indeed our results from extinction simulations suggest large-mammal assemblages with fewer predators are more likely to be stable. However, simplified communities with smaller richness of both predator and prey species were the most stable scenarios. This result agrees with the general theoretical understanding that it is much easier to attain stable dynamics in simpler systems (May 1972). On the other hand such impoverished communities would be vulnerable to species loss, since there is limited redundancy, and extinction cascades may follow the extinction of a given species (Terborgh & Estes 2010). These findings suggest the composition of present-day large-mammal assemblages in the Americas could be the consequence of sequential rearrangements that resulted in communities that are more resilient to small perturbations but so species-poor that became highly vulnerable (Terborgh & Estes 2010).

In our dataset the average number of predator species is greater in North than South American Pleistocene sites. Overall, Pleistocene faunas in North America appear to have had richer predator assemblages, whereas South American faunas had richer large-herbivore assemblages (Fariña 1996; Lyons *et al.* 2004). Although dates for Pleistocene fossils from South America are still sparse compared to North America, existing data indicate that the LQE took longer in South America than it did in North America (Cione *et al.* 2009; Barnosky & Lindsey 2010). Based on our findings on the effects of predators and large herbivores in the dynamics of large-mammal assemblages, we hypothesize that the diversity of large herbivores and the relative lack of predators might have favored stability in South American communities. Thus, our results provide a potential explanation for a LQE pattern that relies upon intrinsic characteristics of ecological communities rather than purely external factors. These intrinsic differences in stability, in turn, could interact with external factors such as differences in the timing of human arrival, to generate the chronology of megafaunal extinctions in Americas.

Our simulations testing the effects of humans on the dynamics of large-mammal assemblages suggest the effect of a large predator such as humans would be greater in Pleistocene assemblages than in modern African assemblages. Pleistocene mammal assemblages in the Americas had a greater diversity of large herbivores than the modern African assemblages. The arrival of a predator capable of feeding on a broad range of prey, including the many Pleistocene large herbivores, would increase connectivity and the proportion of strong interactions, greatly changing the network structure and the dynamics of Pleistocene assemblages. There is compelling archaeological evidence that humans hunted large Pleistocene herbivores (e.g., proboscideans, bison) in the Americas (Surovell & Waguespack 2008; Cione *et al.* 2009), but debate continues about whether human overhunting was the main driver of megafaunal extinction (Alroy 2001; Koch & Barnosky 2006), or if other factors (including habitat alteration driven by humans; Barnosky *et al.* 2004) contributed to the LQE. Our results suggest humans, as predators that were able to exploit a variety of large prey in Pleistocene communities, would promote structural changes in these systems, reducing their ecological stability, which in turn may favor extinction cascades and reduce species persistence. Taken together, our findings reveal that knowledge of the network organization of species interactions may be critical to understanding past and future large extinction events.

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APPENDICES

Table S1. Information on the Pleistocene and modern sites used.

Site	Location	N_{pred}	N_{prey}	Time range
N. America (Pleistocene)				
La Brea Tar Pits (Pit 91; Friscia *et al.* 2008)	California, USA	8	12	0.1-0.01 Ma
American Falls Area (Hopkins *et al.* 1969; Pinsof 1998)	Idaho, USA	7	15	0.1-0.01 Ma
Friesenhahn Cave (Graham 1976; Toomey 1994)	Texas, USA	6	9	0.02-0.01 Ma
Ingleside (Lundelius Jr. 1972)	Texas, USA	5	17	0.01-0.01 Ma
Page-Ladson Site (Aucilla River; Webb 2006)	Florida, USA	5	15	0.01-0.01 Ma
S. America (Pleistocene)				
Guerrero Member – Luján (Tonni *et al.* 1985; Tonni *et al.* 2003)	Buenos Aires, Argentina	5	23	0.8-0.01 Ma
Tarija Basin (Marshall & Sempere 1991; Coltorti *et al.* 2007)	Tarija, Bolivia	6	23	0.04-0.02 Ma
São Raimundo Nonato (Guerin 1991)	Piauí, Brazil	3	13	0.1-0.01 Ma
Talara Tar Seeps (Lemon & Churcher 1961)	Talara Region, Peru	3	9	0.1-0.01 Ma
Africa (modern)				
Serengeti National Park (Baskerville *et al.* 2011)	N Tanzania	5	16	Modern
Kruger National Park (Owen-Smith & Mills 2008)	NE South Africa	5	22	Modern
Mala Mala Reserve (Radloff & Du Toit 2004)	NE South Africa	4	18	Modern

Table S2. Probability of stability (P_{st}) for community matrices representing each site. Columns represent different methods of assigning interaction strengths. Confidence intervals within parentheses.

	P_{st}		
	Random	Asymmetric	Body mass
N. America (Pleistocene)			
La Brea Tar Pits	0.32 (0.29-0.35)	0.68 (0.65-0.71)	0.53 (0.50-0.56)
American Falls Area	0.30 (0.27-0.33)	0.64 (0.61-0.67)	0.48 (0.45-0.51)
Friesenhan Cave	0.56 (0.53-0.59)	0.83 (0.81-0.85)	0.73 (0.70-0.73
Ingleside	0.65 (0.62-0.68)	0.85 (0.83-0.87)	0.69 (0.66-0.68)
Page-Ladson Site	0.56 (0.53-0.59)	0.80 (0.78-0.83)	0.65 (0.62-0.67)
S. America (Pleistocene)			
Guerrero Member - Luján	0.71 (0.68-0.74)	0.88 (0.86-0.90)	0.60 (0.58-0.61)
Tarija Basin	0.53 (0.50-0.56)	0.78 (0.75-0.80)	0.48 (0.45-0.51)
São Raimundo Nonato	0.85 (0.82-0.88)	0.93 (0.92-0.95)	0.89 (0.87-0.91)
Talara Tar Seeps	0.85 (0.83-0.87)	0.95 (0.93-0.96)	0.90 (0.89-0.91)
Africa (modern)			
Serengeti National Park	0.41 (0.38-0.44)	0.68 (0.65-0.71)	0.50 (0.48-0.52)
Kruger National Park	0.47 (0.43-0.50)	0.72 (0.69-0.74)	0.50 (0.47-0.53)
Mala Mala Reserve	0.60 (0.57-0.63)	0.79 (0.77-0.82)	0.66 (0.63-0.69)

Table S3. Average time to return to equilibrium (τ) for community matrices representing each site. Columns represent different methods of assigning interaction strengths. Confidence intervals within parentheses.

	τ		
	Random	Asymmetric	Body mass
N. America (Pleistocene)			
La Brea Tar Pits	4.18 (3.84-4.59)	3.36 (3.21-3.53)	3.58 (3.38-3.78)
American Falls Area	3.87 (3.54-4.27)	3.27 (3.08-3.46)	3.51 (3.31-3.71)
Friesenhan Cave	2.86 (2.71-3.03)	2.41 (2.31-2.50)	2.56 (2.45-2.67)
Ingleside	2.06 (1.97-2.16)	1.91 (1.84-1.98)	2.12 (2.03-2.21)
Page-Ladson Site	2.29 (2.19-2.41)	2.14 (2.07-2.22)	2.30 (2.19-2.41)
S. America (Pleistocene)			
Guerrero Member - Luján	1.91 (1.83-1.99)	1.77 (1.71-1.82)	2.41 (2.28-2.54)
Tarija Basin	2.56 (2.34-2.71)	2.31 (2.20-2.41)	2.95 (2.78-3.12)
São Raimundo Nonato	1.25 (1.21-1.29)	1.26 (1.23-1.29)	1.23 (1.20-1.26)
Talara Tar Seeps	1.30 (1.27-1.34)	1.30 (1.27-1.33)	1.32 (1.28-1.36)
Africa (modern)			
Serengeti National Park	2.56 (2.41-2.73)	2.47 (2.34-2.60)	2.64 (2.47-2.81)
Kruger National Park	2.37 (2.24-2.51)	2.28 (2.18-2.38)	2.64 (2.50-2.78)
Mala Mala Reserve	1.79 (1.72-1.86)	1.80 (1.73-1.87)	1.82 (1.75-1.89)

Table S4. Results of regression models for P_{st}. Each column represents a different method of assigning interaction strengths in the community matrix. Rows show the F-statistic, the determination coefficient (R^2), and estimates for each model parameter. *d.f.* = 8 for all models. * $p < 0.05$; ** $p < 0.001$; *** $p < 0.001$.

	Random	Asymmetric	Body mass
F	66.74***	33.94***	41.16***
R^2	0.92	0.85	0.91
N_{pred}	-115.21***	-64.13***	-77.46***
N_{prey}	_	_	-14.96***
M_{pred}	_	_	_
M_{prey}	288.97***	202.74**	173.081**

Table S5. Results of regression models for τ. Each column represents a different method of assigning interaction effects in the community matrix. Rows show the F-statistic, the determination coefficient (R^2), and estimates for each model parameter. *d.f.* = 8 except for the third model where *d.f.* = 9 . * $p < 0.05$; ** $p < 0.001$; *** $p < 0.001$.

	Random	Asymmetric	Body mass
F	135.20***	63.69***	130.00***
R^2	0.97	0.91	0.92
N_{pred}	0.66***	0.10***	0.48***
N_{prey}	_	_	_
M_{pred}	1.06**	_	_
M_{prey}	-0.92**	-0.16**	_

Table S6. Comparison of P_{st} estimates derived using two different methods. P_{st} and averaged P_{st} over 100 potential matrices ($\overline{P}_{st}$). Interaction strength assignment as a function of body mass.

	P_{st}	$\overline{P}_{st}$
N. America (Pleistocene)		
La Brea tar pits	0.53 (0.50-0.56)	0.52
American Falls Area	0.48 (0.45-0.51)	0.47
Friesenhan cave	0.73 (0.70-0.73	0.72
Ingleside	0.69 (0.66-0.68)	0.67
Page-Ladson site	0.65 (0.62-0.67)	0.67
S. America (Pleistocene)		
Guerrero Member - Luján	0.60 (0.58-0.61)	0.59
Tarija	0.48 (0.45-0.51)	0.51
São Raimundo Nonato	0.89 (0.87-0.91)	0.88
Talara tar seeps	0.90 (0.89-0.91)	0.91
Africa (modern)		
Serengeti National Park	0.50 (0.48-0.52)	0.53
Kruger National Park	0.50 (0.47-0.53)	0.49
Mala Mala Reserve	0.66 (0.63-0.69)	0.66

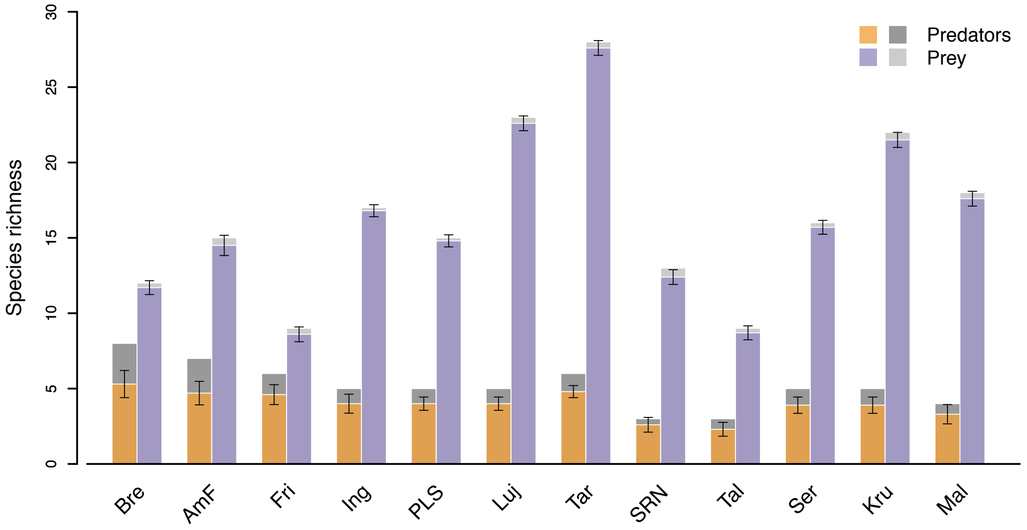

Figure S1. Changes in species composition resulting in the largest change in stability properties for each site. Gray bars depict the original number of predators and prey in each site. Colored bars show the average number of predators and prey after extinction simulations. Error bars tied to the colored bars denote the standard deviation for 100 extinction simulations.

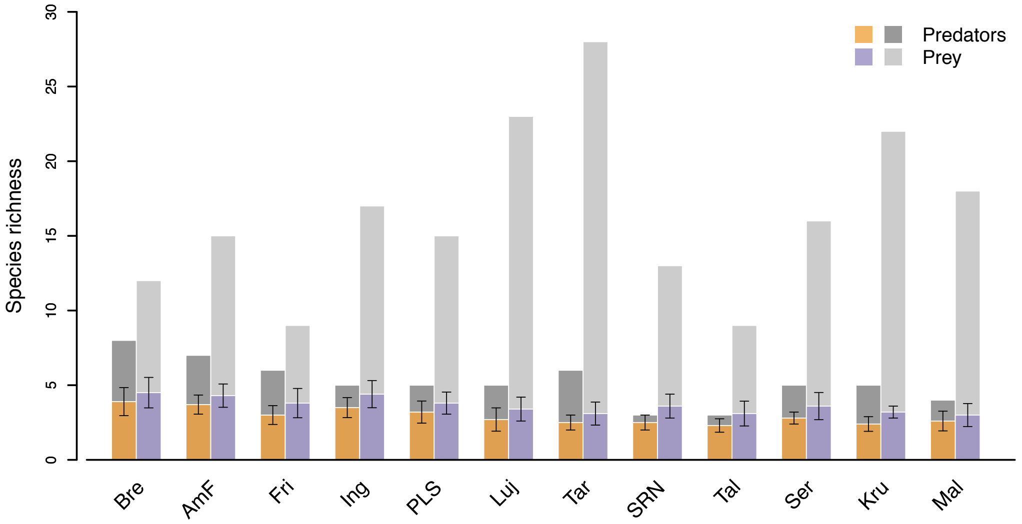

Figure S2. Changes in species composition resulting in the most resilient communities for each site. Gray bars depict the original number of predators and prey in each site. Colored bars show the average number of predators and prey after extinction simulations. Error bars tied to the colored bars denote the standard deviation for 100 extinction simulations.

CAPÍTULO 5

MODELING THE RESPONSE OF A PLEISTOCENE MAMMAL ASSEMBLAGE TO CLIMATE CHANGE AND HUMAN IMPACT

Mathias M. Pires & Paulo R. Guimarães Jr.

Abstract. Pleistocene extinctions depleted the fauna of large vertebrates worldwide. The proposed underlying causes include the effects of climate change, anthropogenic impacts and combinations of both. Despite the arguments in favor or against each set of hypotheses, understanding how the dynamics of Pleistocene assemblages responded to different impacts, and how these changes would affect their composition, is a fundamental step to understand the Pleistocene extinctions. Here we simulated the ecological dynamics of a North American large-mammal assemblage from the Pleistocene, using an allometric predator-prey model, to unravel the potential ways whereby climate change and the arrival of humans could have affected such systems. Our results show species persistence would be impaired by increased competition and reduced carrying capacities, due to climate change. Moreover, we show the impact of a newly arriving predator with wide dietary breadth, such as humans, could be devastating. Our results also point out indirect effects due to interactions mediated by predators and producers may have had an important role in Pleistocene extinctions, reducing populations that were not directly impacted by climatic or anthropic factors. Moreover, our findings on the combined effects of climate change give quantitative support to the most recent assessments on the causes of the LQE, which suggest climate changes could have forced the populations to lower densities whereas humans delivered the final blow determining extinction patterns.

INTRODUCTION

The worldwide extinction of large terrestrial vertebrates by the end of the Pleistocene, between 50,000 and 11,000 years ago, was the Earth's latest great extinction event (Martin & Klein 1984; MacPhee 1999). This episode led to the disappearance of more than 100 large-mammal genera and impacted primarily the Americas and Australia, which lost more than 70% of their large mammalian fauna (Koch & Barnosky 2006). Because extinctions happened at a time climate was fluctuating and the human populations were expanding, the Pleistocene extinctions provide not only the opportunity to better understand how large extinction episodes take place, but to comprehend how the interplay between climactic and anthropogenic impacts affects ecological communities.

All continents experienced climatic fluctuations during late Pleistocene. Climate variability was strong especially during the transition between the Last Glacial Maximum (26.5-19.0 ky BP) and the beginning of the Holocene (11.7 ky BP; Stuart 1991; Barnosky *et al.* 2004; Nogués-Bravo *et al.* 2010). Hypotheses evoking climate changes as the main trigger of megafaunal extinctions suggest the ecological effects of climate change, not the changes in climate per se, would have caused extinctions (Graham & Lundelius 1984; Guthrie 1984; Koch & Barnosky 2006). Climatic fluctuations would have reduced the availability of habitat and resources, thus reducing the populations of large terrestrial vertebrates below a point at which they were not able to recover (Koch & Barnosky 2006; Nogués-Bravo *et al.* 2010). Roughly at the same time, humans were dispersing globally (Bowler *et al.* 2003; Goebel *et al.* 2008).

The arrival and expansion of human populations predates most of the Pleistocene extinctions, what has fueled several hypotheses on the role of anthropogenic impacts on megafaunal extinctions (MacPhee 1999; Burney & Flannery 2005; Koch &

Barnosky 2006; but see Wroe *et al.* 2013). Overkill hypotheses suggest prehistoric humans hunted megafauna to extinction (Martin 1984), but it has been argued humans could also have impacted megafauna indirectly, chiefly due to habitat alteration (Miller *et al.* 2005; Robinson *et al.* 2005).

Most of the studies on the potential causes for the Pleistocene megafaunal extinctions focused on examining the timing of extinctions in relation to the timing of human arrival and climate changes (Martin & Klein 1984; Stuart *et al.* 2004; Guthrie 2006; Prescott *et al.* 2012). Current evidence on the timing of extinctions suggests both climatic and anthropogenic impacts might have contributed (Lorenzen *et al.* 2011; Prescott *et al.* 2012; Lima-Ribeiro *et al.* 2013). Explicit quantitative models testing the potential effects of climate changes on megafaunal extinctions are scant, but several studies used simulations to explore whether the population growth and hunting rates of humans would be able to generate the observed extinction patterns (e.g., Belovski 1988; Alroy 2001; Brook & Bowman 2002, 2004). Collectively these studies show there are different possible scenarios whereby humans could have driven megafauna to extinction (but see Choquenot & Bowman 1998).

Despite the arguments in favor or against each set of hypotheses (see Koch & Barnosky 2006), a fundamental step to understand the Pleistocene extinctions is to investigate how should large-mammal assemblages respond to different types of impact (Ripple & Van Valkenburgh 2010). Species within any assemblage are connected through their interactions, and the effects of any perturbation have the potential to propagate through the system via direct and indirect effects (Terborgh & Estes 2010). Here we used a system of differential equations where life history and ecological attributes are a function of body size to simulate predator-prey dynamics in a North American large-mammal assemblage from late Pleistocene. We simulated different scenarios, such as the arrival of humans as a new predator and increased competition driven by climate change, to understand how the potential triggers of the extinction episode would have changed community dynamics, affecting species persistence.

METHODS

Data

We used data on the species composition and estimated body mass of species found within the La Brea tar pits (Akersten *et al.* 1983). We chose this fossil assemblage as a model system because it bears several of the megafauna species known to have occurred at the same time during late Pleistocene in North America. We consider here only mammalian herbivores weighing more than 5 kg, which are preyed mainly by large predators (Carbone *et al.* 1999), and carnivores with average body mass greater than 20 kg. These cut-off values allow us to define a large-mammal assemblage forming a compartment that is loosely connected, both structurally and dynamically, with the rest of the food web (Terborgh & Estes 2010).

Simulating system dynamics

Biological traits of different organisms scale with body size obeying simple allometric scaling relationships (Damuth 1981; Niklas 2007). Such empirical allometric relationships have been formalized by the metabolic theory, which predicts how metabolic rate, which varies with body size, affects biological processes by constraining the rates of resource use and resource allocation (Peters 1986; Brown *et al.* 2004; Savage *et al.* 2004). To simulate the dynamics of a Pleistocene large-mammal assemblage we used a scaled version of the Rosenzweig-MacArthur predator-prey model in which life history attributes, such as mortality rate and population growth, and ecological attributes such as carrying capacity scale with body size (Weitz & Levin 2006). We generalized the model for *S* species and added competition between primary consumers (equations 1 and 2). Allometric scaling functions and the meaning of each parameter in equations 1 and 2 are presented in Table 1. The reasoning behind each function can be found in Weitz and Levin (2006) and Scheffer and van Nes (2006).

$$\frac{dN_i}{dt} = r_i\left(m_{Ni}\right)N_i\left[1 - \frac{\sum_k \alpha_{ik}\left(m_{Ni}, m_{Nk}\right)N_k}{K_i\left(m_{Ni}\right)}\right] - \frac{\sum_j \phi_{ij}\left(m_{Ni}, m_{Pj}\right)N_i P_j}{1 + \sum_j \sum_i N_i \big/ N_0\left(m_{Ni}, m_{Pj}\right)} \qquad (1)$$

$$\frac{dP_j}{dt} = \frac{\sum_i \varepsilon_{ij}\left(m_{Ni}, m_{Pj}\right)\phi_{ij}\left(m_{Ni}, m_{Pj}\right)N_i P_j}{1 + \sum_i N \big/ N_0\left(m_{Ni}, m_{Pj}\right)} - d_j\left(m_{Pj}\right)P_j \qquad (2)$$

Table 1. Model parameters and scaling functions. m_N is the body mass of prey and m_P the body mass of predators.

Parameters/functions	Meaning	Scaling
r	Intrinsic growth rate	$m_N^{-1/4}$
α	Competition coefficient	$\frac{\int_{-\infty}^{\infty} P_i(L)P_j(L)dL}{\int_{-\infty}^{\infty} P_i(L)^2 dL}$, where $P(L)$ is a Gaussian depicting resource use along an axis L
K	Carrying capacity	$m_N^{-3/4}$
ϕ	Predation function	$\left[\frac{e^{\kappa}}{1+e^{\kappa}}\right]\left[m_P^{\beta}F\left(\frac{m_P}{m_N}\right)\right]$, where $\kappa = a + b\log\left(\frac{m_N}{m_P}\right) + c\log^2\left(\frac{m_N}{m_P}\right)$ and $F(x) \sim \begin{Bmatrix} x^{-\beta} & x < 0.1 \\ 1 & x \geq 0.1 \end{Bmatrix}$
N_o	Half saturation	$m_P^{3/4} \big/ \left(m_N \phi\right)$

ε	Conversion efficiency	m_N / m_P
d	Death rate	$m_P^{-1/4}$

Body size controls not only resource use and allocation but also constrains foraging behavior since it determines the size limits of potential prey of a given predator, thus affecting the rate of biotic interactions (Emmerson & Raffaelli 2004; Brose 2010). Empirical data suggest there is often a hump-shaped relationship between attack rate and predator-prey body-mass ratios (Brose 2010). Moreover, dietary breadth of carnivores is often positively related to body size (Sinclair *et al.* 2003). Thus, we used a statistical model based on body mass ratios (Rohr *et al.* 2010) to parameterize the interaction probability between predators and prey, which is embedded in the function ϕ in the differential equations 1 and 2 (Table 1). This statistical model relating interaction probability and body mass ratios has been shown to be effective in predicting predator-prey interactions between large mammals in the African savannah[3]. Therefore by using such model we include a realistic structure for predator-prey interaction patterns among mammalian species. We parameterized the log ratio model using the range of values that maximize the model goodness of fit for interactions between African large mammals[3]. Therefore, we assume that similar rules govern how body-size relationships translate into interaction patterns in the Pleistocene and modern large-mammal assemblages, as often assumed in paleoecological studies with Pleistocene megafauna. By doing that, in our simulations large predators will interact more frequently with medium- and large-sized prey than

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[3] Capítulo 3 – The disruption of predator-prey interaction networks after megafaunal extinctions

with small prey. Accordingly, small-sized predators are more likely to interact with smaller prey than with large prey.

We also used body-mass relationships to estimate the competition coefficient, α, between prey species. Assuming we can order species along an axis representing a niche dimension, competition should be higher for species with higher niche overlap. Thus, following Scheffer and Van Nes (2006) we first ordered prey species along an axis according to body mass. The position of each species along the axis determines the mean of a distribution depicting resource use. Therefore, we assumed species of similar body size are more likely to share similar resources. Then, we sampled n values from a normal distribution with parameters $\mu = 0.1$ and $\sigma = 0.1$ and assigned the absolute values as the niche widths of each of the n prey species. Niche widths were assigned according to body mass, i.e., assuming larger species have more diverse diets. Because there's conflicting evidence for the relationship between body mass and niche width of large terrestrial herbivores (Hansen *et al.* 1985; Dobson *et al.* 2009) we also tested the robustness of our results by assigning niche widths at random. After assigning niche widths we used the framework proposed by Scheffer and Van Nes (2006) to estimate competition coefficients from niche overlap along a finite linear niche axis.

Baseline simulations

We performed all numerical simulations using an ordinary differential equation solver in MATLAB® environment. We sampled initial population densities from uniform distributions ranging from 0.7 to 1 for prey and 0.05 to 0.2 for predators so that initial density of predator populations is smaller than that of prey. A system modeled with that many parameters and several species is unlikely to have easily identifiable equilibrium points. Moreover, evidence shows populations continuously fluctuate suggesting the transient dynamics are important in understanding how natural systems behave (Hastings 2001). For this reason we opted to analyze the dynamic behavior of the community for a fixed amount of timesteps ($T = 200$).

Although most of the parameters of the dynamic model are fixed by the allometric scaling relationships, some of them have more empirical support than others. The mortality rates of mammals, for instance, seem to be consistently lower than that of ectothermic organisms (Mccoy & Gillooly 2008), which are overrepresented in the tests of the empirical scaling relationship. We also have limited information on how resource use patterns translate into competition, especially for large herbivores for which the relevance of interspecific competition has been subject of debate (Sinclair & Norton-Griffiths 1982; Mcnaughton & Georgiadis 1986). Therefore we included two additional parameters, β_0 and β_1, to rescale predator mortality rate, d, and the competition coefficients α, respectively. We ran the simulations varying these parameters between 0.1 and 1, by 0.05, (10^3 simulations for each), and registered the number of extinct species at the end of 200 timesteps. We then used in the subsequent simulations the values of β_0 and β_1 found to minimize the average number of extinctions. By minimizing the number of extinctions in baseline simulations we are more confident we are modeling a plausible scenario, since assemblages like the one we model here seem to have existed for a long time before the LQE. Moreover, we guarantee that most extinctions after simulating human arrival or climate change are a consequence of these factors.

Persistence and coexistence

To summarize the dynamics of the community under different scenarios we measured two main components of system stability: persistence and coexistence. To evaluate persistence we registered the number of species that died out after each simulation under each scenario. As a measure of the probability of coexistence we registered the proportion of time steps within each simulation in which all starting species coexisted.

We also registered the frequency with which each species went extinct, considering all simulations under each scenario (see below), to obtain an estimate of the probability of extinction. To allow the comparison of extinction patterns generated under the different simulated scenarios we used the extinction patterns of the LQE as a benchmark. We developed an index that considers the odds that simulations under a given scenario correctly predict the extinction or survival of each species:

$$C = \frac{1}{2}\left[\frac{\sum_i f_i E_i}{\sum E} + \frac{\sum_i (1 - f_i)(1 - E_i)}{\sum 1 - E}\right] \quad (3),$$

where f_i is the proportion of simulations, under a given scenario, in which species i went extinct and E_i equals 1 when i is extinct and 0 if i is extant. A C value equal to 1 would indicate that a given scenario correctly predicts extant and extinct species in all simulations. We are aware this approach has limitations. Extinction in our model is a local phenomenon and does not necessarily imply in regional or global extinction. Our models do not include, dispersal or any spatially structured processes, which are especially important if we are considering the extinction of a species in regional or global scale. However, assuming species most likely to go extinct locally are those most likely to go extinct globally is reasonable. Therefore, computing C allows us to assess whether the mechanisms simulated here in local scale would be plausible drivers of the LQE extinction patterns.

The relevance of trophic structure

Species are connected to each other through their interactions and thus are likely to directly or indirectly affect each other. In this sense the structure of trophic interactions should be important to determine dynamics, and, more specifically, how the system responds to different impacts (McCann 2011). To test the relevance of trophic structure for system dynamics we ran 100 simulations and for each of those we randomly redistributed the probabilities of interaction between predator and prey species (100 randomizations each) in order to break the relationship between interaction patterns and body mass ratios. We then compared the distributions of the response variables with that of baseline simulations.

The effect of climate changes

Among the potential effects of climate changes are the loss of natural habitats and vegetation shifts, which decrease resource availability (Guthrie 1984; Barnosky 1986; Guthrie 2006). Therefore, we simulated two potential effects of climate change: (i) increase in the niche overlap between herbivores; (ii) the reduction of carrying capacities of prey populations. In such scenarios we did not model producers explicitly, but simulated possible consequences of fluctuations in resource availability for herbivores. Moreover, the effects of climate change over predators are solely indirect, through changes in prey availability.

For simplicity we assume the increase in niche overlap and the reduction in carrying capacities to be proportional across all prey species. Thus, to simulate increases in niche overlap we incremented by 10% to 300% (increasing by 10%) the mean of the distribution from which the values of niche widths were sampled. We performed 10^3 simulations for each increment in the mean of the distribution. The effect of increasing niche overlap could be constrained because we rescaled competition (using β_1; see *Baseline simulations*) to reduce extinctions in the baseline simulations. To test how the scaling of competition affected our overall results we reran the simulations while considering the baseline competition is twice as large as considered originally. To simulate the effect of decreasing carrying capacities of herbivores we reduced a fraction (10% to 90% decreasing by 10%) of the carrying capacity originally computed from the allometric scaling. Again, we performed 10^3 simulations for each percent decline in carrying capacities.

Human impact

Previous studies on the overkill hypotheses tested the potential of humans to hunt megafauna to extinction by simulating the population dynamics of megafauna herbivores and humans while considering specific aspects of human ecology (e.g., Alroy 2001; Brook & Bowman 2004). Our focus here is not to test whether humans would be able to hunt megafauna to extinction on a continental scale. Also, we are aware the arrival of humans could have had different impacts over Pleistocene populations, including indirect impacts through habitat alteration (Koch & Barnosky 2006). Here we aimed at understanding how humans, as a new predator joining a Pleistocene large-mammal assemblage, would affect the ecological dynamics of the system locally. Therefore, we tested the potential effects of humans by comparing the dynamics of the large-mammal assemblage with and without humans. As done for the other predators the population parameters of humans were a function of body mass, set as 70 kg. To test the effects of different possible hunting behaviors we ran simulations changing the interaction coefficient of humans with prey species. By changing the body mass input for humans in function ϕ, which represents predation rates, we varied the optimum prey size (17.5, 35, 70, 140, 280, 560, 1120, 2240, and

4480 kg) for humans while keeping the remaining parameters fixed as a function of actual human body mass (70 kg). In each simulation we sampled the initial population size of humans from the same distribution used for other predators. We ran 10^3 simulations for each optimum prey size.

The combined effect of humans and climate

We tested the combined effect of humans and climate change by simulating each climate effect scenario of increased interspecific competition under the different scenarios that included humans. We then registered persistence, coexistence and extinction patterns for each combination. We ran 10^3 simulations for each combination.

RESULTS

Our simulations always resulted in a few species going extinct, even in the baseline simulations (Fig. 1). In the baseline simulations species that went extinct were the smallest predators, which probably fed upon alternative, smaller, prey that are not included in our analysis. When compared to a theoretical scenario in which allometric scaling of life history attributes is kept the same, but interaction patterns are randomly determined, the scenario in which body size shapes interaction patterns yields larger persistence (Fig 1), suggesting that size-based interactions favor coexistence in networks formed by large mammals.

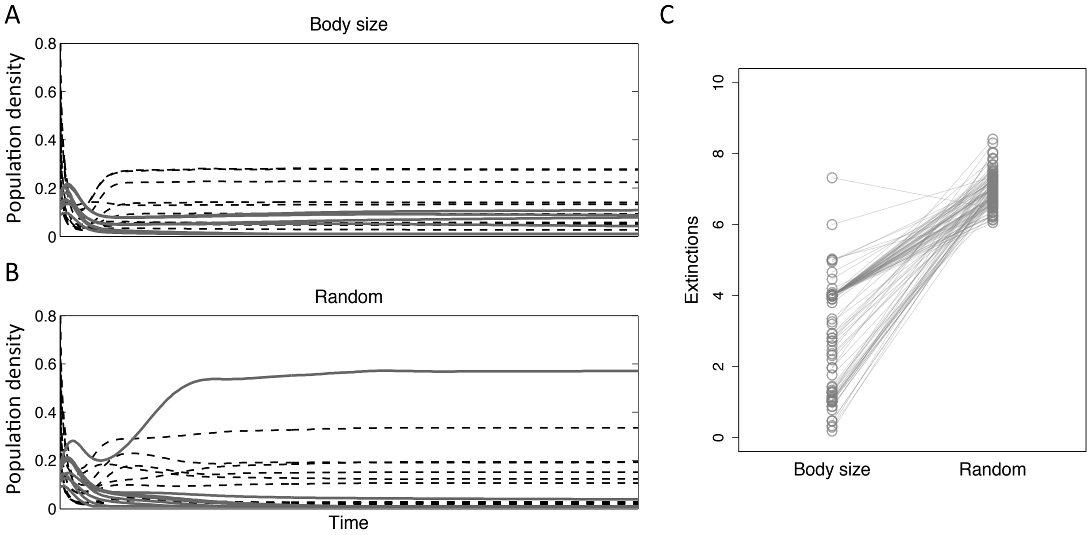

Figure 1. Comparing the effect of realistic predator-prey interaction patterns determined by body size (**A**) against randomized interaction patterns (**B**). **A** and **B** show population densities over time. Gray solid lines represent predators and dashed lines represent prey species. **C**) Number of extinctions under the two scenarios (10^2 simulations with the same initial conditions).

Our simulations of climate-driven changes in resource availability, by increasing niche overlap or reducing the carrying capacity of prey populations, reduced the overall density of prey. As expected, simulations of climate change reduced persistence and coexistence when compared to baseline simulations (Fig. 2A and 2B; Table S1). For instance, when the average niche width of prey species was twice as large as that in baseline simulations, the mean number of extinctions increased from 3 to 5 and the probability of coexistence reduced from 0.5 to 0.3. Although we simulated climate change by altering the parameters of prey populations, the increase in the probability of extinction of predators was much greater than the changes in the probability of extinction of herbivores themselves (Fig. 3A). Under the scenarios of increased competition between prey species, a two-fold increase in the average niche width of herbivores was enough to drive all predators to extinction in all simulations

(Fig. 3A). If the carrying capacities are halved, the effect is similar and all predators die out (Fig. 3B). Additional analyses where we considered a greater baseline competition or where niche widths were assigned independently from body mass yielded qualitatively similar results (Table S2).

The addition of humans produced more variable results. Adding a new predator, such as humans, to the system also reduced persistence and coexistence when compared to the baseline simulations. However, different hunting behaviors resulted in very different dynamics and extinction patterns. For instance, including humans targeting preferably prey species weighting around 17 kg the mean number of extinctions increased from 3 to 4.5, whereas humans targeting prey around 200 kg increased the number of extinction to 18 and decreased the probability of coexistence from 0.5 to 0.1 (Fig 2C and Table S1). Changing from humans more likely to prey on smaller herbivores, to humans targeting large game - passing through more generalized hunting patterns - persistence and coexistence followed a hump-shaped relationship (Fig. 2C). Prey species and large predators were more likely to survive and small predators more likely to die out when we simulated humans targeting smaller prey. Simulating humans preying preferably on the largest prey species increased the probability of extinction for preferred prey, but smaller predators and prey species became less likely to go extinct (Fig 3). When humans targeted prey of intermediate size nearly all species had a high probability of dying out.

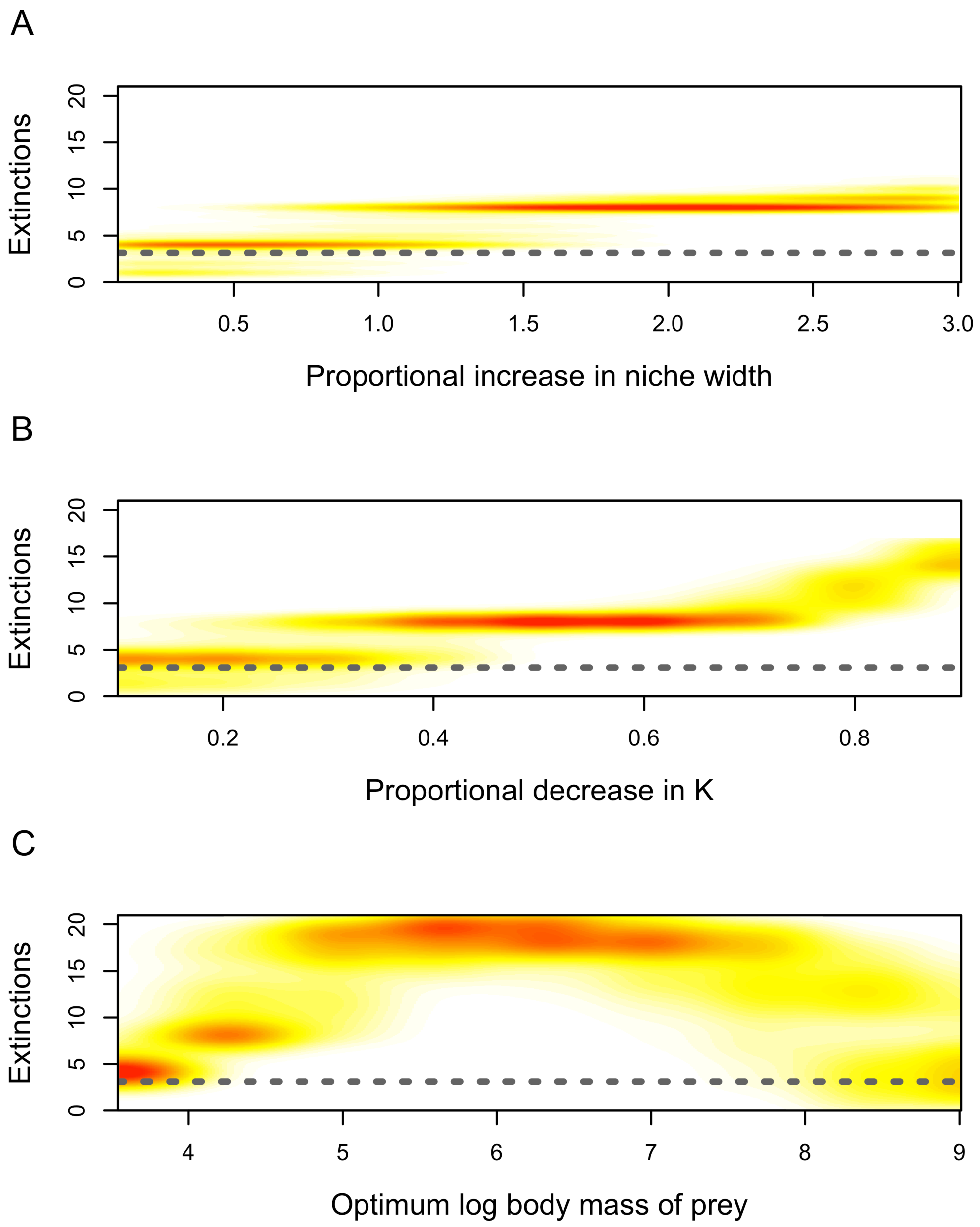

Figure 2. Number of extinctions under each simulated scenario. A and B simulate possible effects of climate change. **A** shows the number of extinctions in simulations where we increased the niche width of prey species. **B** depicts extinctions after decreasing the carrying capacity, *K*, of herbivores. **C** shows how the number of extinctions varies for simulations with humans targeting prey of different sizes. Colors portray the density of points considering 10^3 simulations under each scenario. The gray dotted line shows the average number of extinctions in 10^3 baseline simulations.

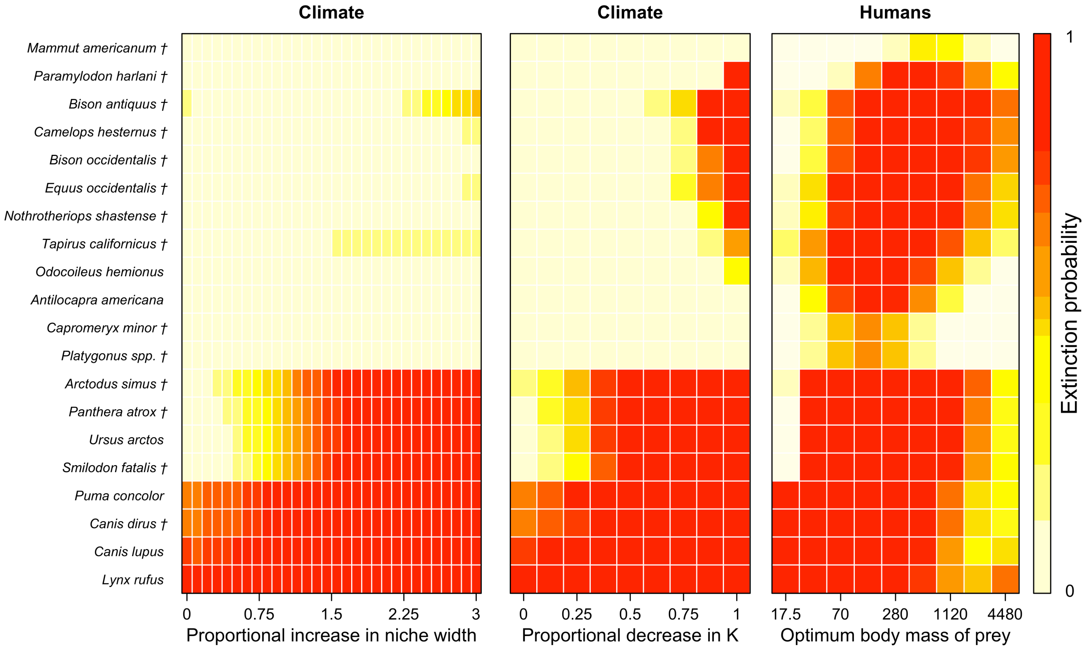

Figure 3. Probability of extinction of each species under each simulated scenario: increasing niche widths of prey, reduced carrying capacity of prey, and arrival of humans targeting prey of different sizes. † signals extinct species.

If we compare the results of our simulations on the effects of climate change and introduction of humans, the later produced more abrupt changes in system dynamics (Fig. 2). Even when we increased the magnitude of competition, by setting β_o twice as large as the value found to minimize extinctions in baseline simulations (see *climate change effects* under Materials and Methods), the effects of increasing niche widths, relative to baseline simulations, were smaller than the effects of human arrival (Fig S1). Some scenarios including humans as large-game hunters produced extinction patterns more similar to the extinctions patterns of the LQE ($C > 0.5$) than scenarios simulating climate change effects ($C \sim 0.3$) or those that included humans targeting smaller prey species ($C \sim 0.3$; Table S1). Interestingly, the largest extinct herbivore in our data set, the American mastodon (*Mammutt americanum*), had small probability of extinction under all scenarios (Fig. 3).

When we combined both the increase in niche width of prey and the addition of a predator species, simulating the combined effects of climate change and human arrival, we found increasing niche overlap decreased persistence when humans targeted primarily smaller prey (Fig. 4). However, for humans targeting preferably prey > 70 kg, the effects of increasing niche widths were negligible (Fig. 4). Thus, the extinction patterns resulting from our simulations seem to be driven qualitatively by humans, but may be quantitatively affected by the effects of climate change simulated here (Fig. S2).

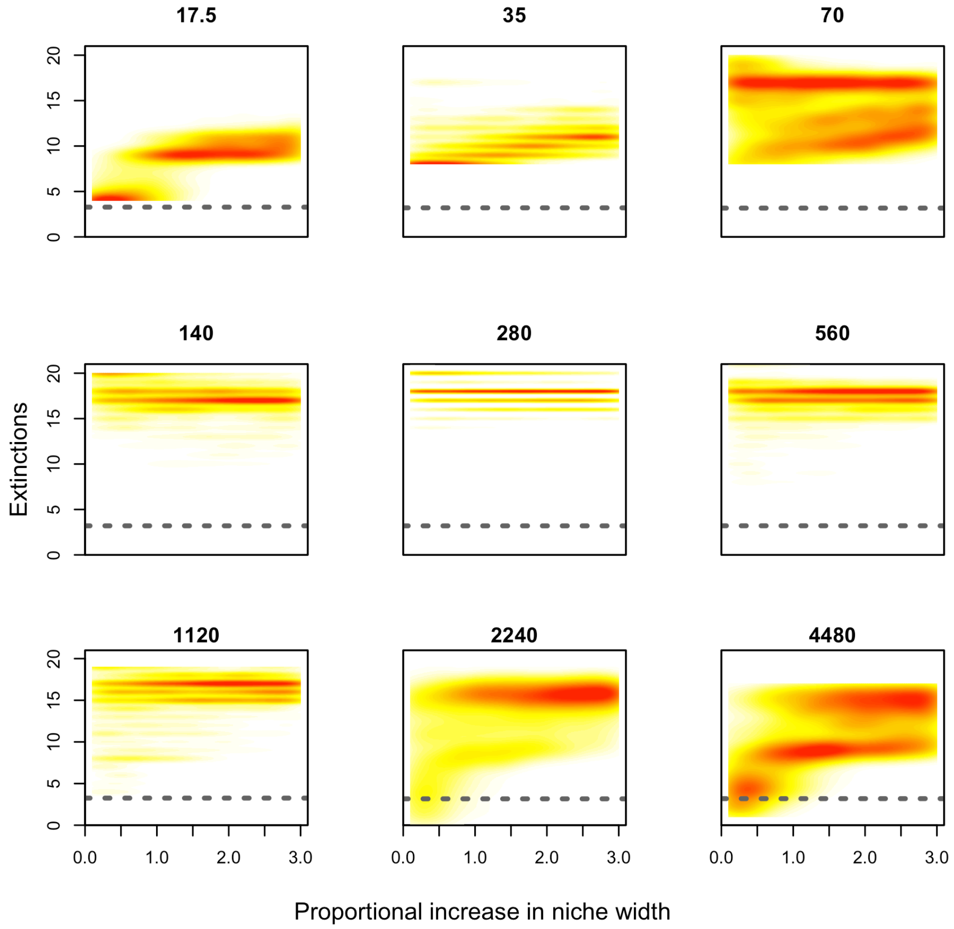

Figure 4. Number of extinctions when combining the simulated effect of climate change and human arrival. Each panel depicts how the number of extinctions varies with increasing niche width under each scenario of human hunting behavior (optimum prey size ranging from 17.5 kg to 4480 kg; above each panel).

DISCUSSION

Our simulations allowed us to assess how important are interaction patterns to understand the dynamics of large-mammal assemblages and to examine how processes related to LQE hypotheses would have affected Pleistocene assemblages. Randomizing the interaction patterns determined by body-size relationships between predator and prey significantly impacted dynamics, reducing species persistence. These results emphasize the value of considering the way interactions are organized when studying system dynamics. Moreover, our findings suggest the constraints imposed by body-mass relationships in foraging behavior favor persistence and may promote coexistence in rich assemblages (Brose *et al.* 2006). Interactions modulate how perturbations such as the effect of climate change and the arrival of a new predator propagate through the system affecting species trough direct and indirect effects.

By simulating some of the potential impacts of climate change and human arrival in a model Pleistocene large-mammal assemblage we were able to examine the plausibility the LQE hypotheses in a local context. As expected, our results show the effects of climate change and the arrival of humans, as we modeled here, are likely to reduce species persistence and the likelihood of coexistence over time. Yet, the specific responses of the assemblage studied here to each scenario differed substantially. The increase in the niche widths and decrease in carrying capacities of prey populations reduced their final densities, and frequently led to the extinction of predators. The response of predators to increased competition between prey species underscores the importance of indirect effects in the dynamics of the assemblage (Wootton 1994). Although we are not modeling producers explicitly, our climate change scenarios simulate the reduction of resource availability for herbivores. Thus, the resulting extinctions of predators can be interpreted as indirect bottom-up effects spreading across trophic levels (Terborgh & Estes 2010). The potential relevance of competition and indirect effects in Pleistocene extinctions has been acknowledged before (Guthrie 1984; Owen-Smith 1999). Here we modeled possible effects of climate change and showed how competition and indirect effects could have contributed to reduce the populations of predator and prey species in Pleistocene assemblages.

Human arrival also impacted persistence, but produced more variable results. Although considering humans that hunt preferably smaller (< 40 kg) prey species had little effect on the overall patterns, a predator targeting larger prey markedly affected the dynamics, and ultimately the composition, of the assemblage. The addition of a predator targeting species between 100 and 1000 kg resulted in the extinction of almost all species except for two or three herbivores. In simulations where humans preferred prey species weighing more than 1,000 kg, however, the overall impact on the assemblage was reduced. Large predators and medium-sized prey ended up extinct, but smaller prey and predators were more likely to survive, a scenario more similar to what happened with the North American large mammals (Martin & Klein 1984; Barnosky *et al.* 2004). The main pathway by which the added species impact dynamics is, again, by decreasing prey densities. However, a predator that exploits intermediate body sizes is less likely to decline even after reducing the density of preferred prey, since there are several fallback prey species that prevent its density from crashing (Ripple *et al.* 2010). As a result, the addition of a predator that targets the medium-sized prey in our simulations creates a scenario of apparent competition where prey populations are overexploited. Apparent competition mediated by predators, occurs, when prey species negatively affect each other, by enhancing the equilibrium density of shared predators (Chaneton & Bonsall 2000). Both theoretical and empirical evidence suggest apparent competition increases the potential of overexploitation and, ultimately, extinction in modern systems (Holt 1977; Bonsall & Hassell 1997). Additionally, by reducing the availability of prey, humans preying upon medium-sized prey compete with other predators, increasing the likelihood they go extinct in the simulations as well. A similar mechanism, whereby humans preferring large prey would have triggered Pleistocene extinctions through indirect effects, has been proposed by Ripple and Van Valkenburgh (2010). Here we showed through our simulations this mechanism is plausible and we identified a set of conditions in which extinctions are likely to occur and which would be the most vulnerable species.

There is unequivocal evidence that paleoindians hunted large prey (Buchanan 2006; Surovell & Waguespack 2008), and foraging models suggest paleoindians should pursue a wide range of potential prey (Byers & Ugan 2005). The extinctions caused by predators invasions in historical times such as predatory fishes in lakes (Pelicice & Agostinho 2009), foxes in Australia (Kinnear *et al.* 2002), and domestic cats in islands (Donlan & Wilcox 2008) show how devastating can the arrival of an allochthonous generalist predator be. Yet, one of the most debated topics related to the hypotheses pointing humans as the cause of extinctions is how small populations of hunters with primitive technologies could have led so may species to extinction (Stuart 1991). We show here that regardless of the density of human populations, Pleistocene large-mammal assemblages should be strongly impacted by the arrival of a large predator, at least on a local scale. These findings agree with Alroy's (2001) in that there is no need to assume exceptionally high population growth rates or attack rates to generate a scenario where several species go extinct: the arrival of a new predator with wide dietary breadth in an established assemblage is enough to result in many extinctions. Our findings cannot unambiguously point in the direction of humans as the immediate cause of megafaunal extinctions. However, here we go one step further by showing how the arrival of a new predator could drastically impact ecological dynamics affecting not only its prey species, but indirectly affect other herbivores and predators.

Our results simulating the combined effects of climate change and anthropogenic impacts, show the impact of an allochthonous predator in the assemblage may be aggravated by bottom-up forcing driven by climate changes. Yet, extinction patterns were determined chiefly by the addition of a predator. These results agree with the most recent assessments on the causes of the LQE in North America, which suggest climate changes could have forced the populations to lower densities and humans delivered the final blow (Barnosky *et al.* 2004; Barnosky 2008; Prescott *et al.* 2012; Lima-Ribeiro *et al.* 2013).

Even though some of the modeled scenarios accurately predict species that went extinct and species that survived, we modeled here the dynamics of a local assemblage and extinctions should not be interpreted as the regional or global extinction of a given species. The next step in understanding the underlying mechanisms of the LQE is to unravel how these local processes could have scaled contributing to the extinction patterns in larger scales. A few species that did go extinct in the LQE, such as the American mastodon and peccaries had low probability of extinction under any of the simulated scenarios. Here we only included information on the body mass of each species, which was used to parameterize the model. We did not distinguish, for instance, among browsers and grazers, an important aspect of herbivore ecology structuring competition (Mcnaughton & Georgiadis 1986) and patterns of predation (Yeakel *et al.* 2012) that could have affected how species experienced late Pleistocene impacts (Koch & Barnosky 2006). Moreover, the fact that even in baseline simulations a few species may go extinct suggests some processes that help to maintain viable populations may have been left out. Our modeling framework does not include, for example, processes related to spatial heterogeneity and dispersal, which may increase the likelihood of coexistence and persistence (Kareiva 1990). Incorporating other layers of biological realism and examining how extinction patterns are impacted may reveal the relative importance of diet variation, spatial heterogeneity and metapopulation dynamics in understanding the role of the intrinsic dynamics of large-mammal assemblages in the LQE.

Taken together, our results allowed us to test the plausibility of some hypotheses on the mechanisms underlying the LQE at the level of local assemblages. Assessments like ours, aiming to understand how the intrinsic dynamics of local assemblages in the past could have contributed to their collapse are crucial before extrapolating to understand the mechanisms driving past and on-going extinctions at larger scales.

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APPENDICES

Table S1. Dynamics of a Pleistocene large-mammal assemblage under different scenarios. Average values (± standard deviation) for the probability of coexistence and number of extinct species in 10^3 simulations. *C* measures the accuracy in predicting LQE extinction patterns under each scenario.

Climate effect on niche width			
Proportional increase in niche widths	Coexistence	Extinctions	*C*
0.1	0.47 ± 0.16	3.22 ± 1.48	0.33
0.2	0.48 ± 0.19	3.11 ± 1.51	0.33
0.3	0.44 ± 0.17	3.39 ± 1.56	0.33
0.4	0.43 ± 0.17	3.48 ± 1.55	0.33
0.5	0.41 ± 0.17	3.70 ± 1.67	0.32
0.6	0.39 ± 0.17	3.92 ± 1.82	0.32
0.7	0.36 ± 0.15	4.34 ± 1.84	0.31
0.8	0.35 ± 0.14	4.53 ± 2.02	0.31
0.9	0.32 ± 0.13	5.03 ± 2.09	0.31
1	0.30 ± 0.11	5.25 ± 2.06	0.31
1.1	0.29 ± 0.11	5.70 ± 2.10	0.31
1.2	0.27 ± 0.09	6.06 ± 2.06	0.31

1.3	0.26 ± 0.07	6.56 ± 1.92	0.31
1.4	0.24 ± 0.05	6.87 ± 1.77	0.31
1.5	0.24 ± 0.06	7.22 ± 1.61	0.31
1.6	0.23 ± 0.04	7.44 ± 1.42	0.31
1.7	0.23 ± 0.03	7.67 ± 1.26	0.31
1.8	0.22 ± 0.03	7.81 ± 1.16	0.31
1.9	0.22 ± 0.03	7.96 ± 0.91	0.32
2	0.22 ± 0.03	8.12 ± 0.72	0.32
2.1	0.22 ± 0.03	8.13 ± 0.81	0.32
2.2	0.22 ± 0.02	8.18 ± 0.66	0.32
2.3	0.21 ± 0.02	8.25 ± 0.65	0.32
2.4	0.21 ± 0.02	8.32 ± 0.62	0.32
2.5	0.21 ± 0.02	8.40 ± 0.64	0.32
2.6	0.21 ± 0.02	8.45 ± 0.70	0.32
2.7	0.21 ± 0.02	8.59 ± 0.77	0.33
2.8	0.21 ± 0.02	8.69 ± 0.83	0.33
2.9	0.21 ± 0.02	8.87 ± 0.95	0.34
3	0.21 ± 0.02	9.03 ± 1.06	0.35

Climate effect on carrying capacity (*K*)

Proportional decrease in *K*	Coexistence	Extinctions	*C*
0.1	0.43 ± 0.15	3.43 ± 1.51	0.32
0.2	0.37 ± 0.12	4.02 ± 1.81	0.32
0.3	0.31 ± 0.09	5.15 ± 2.17	0.31
0.4	0.26 ± 0.05	6.97 ± 1.77	0.31
0.5	0.24 ± 0.02	7.97 ± 0.53	0.31
0.6	0.23 ± 0.02	8.18 ± 0.59	0.32
0.7	0.21 ± 0.03	8.93 ± 1.24	0.34

0.8	0.18 ± 0.01	11.49 ± 1.44	0.43
0.9	0.16 ± 0.01	14.71 ± 1.18	0.50
Effect of adding humans			
Optimum body mass of human prey (kg)	Coexistence	Extinctions	*C*
17.5	0.32 ± 0.09	4.63 ± 1.67	0.29
35	0.21 ± 0.04	10.55 ± 3.47	0.31
70	0.16 ± 0.03	15.89 ± 3.55	0.37
140	0.14 ± 0.01	18.59 ± 1.63	0.43
280	0.14 ± 0.02	18.54 ± 1.67	0.44
560	0.14 ± 0.02	17.15 ± 2.76	0.49
1120	0.17 ± 0.07	14.03 ± 4.30	0.58
2240	0.26 ± 0.20	9.26 ± 5.26	0.61
4480	0.31 ± 0.16	6.01 ± 3.99	0.52

Table S2. Climate effect on the dynamics of a Pleistocene large-mammal assemblage under different assumptions. Average values (± standard deviation) for the probability of coexistence and number of extinct species in 10^3 simulations. *C* measures the accuracy in predicting LQE extinction patterns under each scenario.

Climate effect on niche width									
	Baseline			Greater competition			Random niche width		
Proportional increase in niche widths	Coexistence	Extinctions	*C*	Coexistence	Extinctions	*C*	Coexistence	Extinctions	*C*
0.1	0.47 ± 0.16	3.22 ± 1.48	0.33	0.24 ± 0.05	7.48 ± 2.98	0.48	0.27 ± 0.06	5.76 ± 1.18	0.34
0.2	0.48 ± 0.19	3.11 ± 1.51	0.33	0.24 ± 0.05	8.16 ± 2.89	0.47	0.26 ± 0.05	5.88 ± 1.24	0.35
0.3	0.44 ± 0.17	3.39 ± 1.56	0.33	0.23 ± 0.05	8.72 ± 2.84	0.45	0.25 ± 0.05	6.06 ± 1.32	0.35
0.4	0.43 ± 0.17	3.48 ± 1.55	0.33	0.23 ± 0.04	9.15 ± 2.58	0.44	0.25 ± 0.05	6.22 ± 1.44	0.35
0.5	0.41 ± 0.17	3.70 ± 1.67	0.32	0.22 ± 0.05	9.67 ± 2.34	0.43	0.24 ± 0.05	6.53 ± 1.59	0.36
0.6	0.39 ± 0.17	3.92 ± 1.82	0.32	0.22 ± 0.04	9.96 ± 2.21	0.43	0.24 ± 0.05	6.85 ± 1.76	0.36
0.7	0.36 ± 0.15	4.34 ± 1.84	0.31	0.21 ± 0.03	10.29 ± 1.94	0.41	0.23 ± 0.04	7.27 ± 1.96	0.36
0.8	0.35 ± 0.14	4.53 ± 2.02	0.31	0.21 ± 0.03	10.61 ± 1.72	0.41	0.22 ± 0.04	7.62 ± 2.02	0.37
0.9	0.32 ± 0.13	5.03 ± 2.09	0.31	0.20 ± 0.03	10.83 ± 1.58	0.39	0.22 ± 0.04	7.94 ± 2.14	0.37
1	0.30 ± 0.11	5.25 ± 2.06	0.31	0.20 ± 0.03	11.02 ± 1.57	0.39	0.22 ± 0.04	8.37 ± 2.15	0.38
1.1	0.29 ± 0.11	5.70 ± 2.10	0.31	0.20 ± 0.03	11.28 ± 1.49	0.38	0.21 ± 0.04	8.91 ± 2.16	0.39
1.2	0.27 ± 0.09	6.06 ± 2.06	0.31	0.19 ± 0.03	11.57 ± 1.66	0.36	0.21 ± 0.04	9.22 ± 2.05	0.39
1.3	0.26 ± 0.07	6.56 ± 1.92	0.31	0.19 ± 0.03	11.83 ± 1.66	0.35	0.20 ± 0.03	9.55 ± 1.99	0.39

1.4	0.24 ± 0.05	6.87 ± 1.77	0.31	0.18 ± 0.03	12.20 ± 1.70	0.35	0.20 ± 0.03	10.08 ± 1.83	0.40
1.5	0.24 ± 0.06	7.22 ± 1.61	0.31	0.18 ± 0.02	12.68 ± 1.87	0.34	0.20 ± 0.03	10.32 ± 1.75	0.40
1.6	0.23 ± 0.04	7.44 ± 1.42	0.31	0.17 ± 0.02	12.96 ± 1.91	0.33	0.20 ± 0.03	10.50 ± 1.67	0.41
1.7	0.23 ± 0.03	7.67 ± 1.26	0.31	0.17 ± 0.02	13.35 ± 1.83	0.33	0.19 ± 0.02	10.81 ± 1.44	0.41
1.8	0.22 ± 0.03	7.81 ± 1.16	0.31	0.17 ± 0.02	13.70 ± 1.83	0.34	0.19 ± 0.02	10.99 ± 1.45	0.42
1.9	0.22 ± 0.03	7.96 ± 0.91	0.32	0.17 ± 0.02	14.10 ± 1.88	0.33	0.19 ± 0.02	11.16 ± 1.34	0.42
2	0.22 ± 0.03	8.12 ± 0.72	0.32	0.17 ± 0.02	14.39 ± 1.86	0.34	0.19 ± 0.02	11.32 ± 1.31	0.43
2.1	0.22 ± 0.03	8.13 ± 0.81	0.32	0.16 ± 0.02	14.85 ± 1.70	0.34	0.19 ± 0.02	11.40 ± 1.30	0.43
2.2	0.22 ± 0.02	8.18 ± 0.66	0.32	0.16 ± 0.02	15.21 ± 1.62	0.35	0.19 ± 0.02	11.49 ± 1.23	0.43
2.3	0.21 ± 0.02	8.25 ± 0.65	0.32	0.16 ± 0.01	15.52 ± 1.57	0.36	0.19 ± 0.02	11.65 ± 1.20	0.44
2.4	0.21 ± 0.02	8.32 ± 0.62	0.32	0.16 ± 0.01	15.77 ± 1.43	0.36	0.19 ± 0.02	11.68 ± 1.23	0.44
2.5	0.21 ± 0.02	8.40 ± 0.64	0.32	0.16 ± 0.01	16.01 ± 1.33	0.37	0.19 ± 0.02	11.76 ± 1.18	0.44
2.6	0.21 ± 0.02	8.45 ± 0.70	0.32	0.16 ± 0.01	16.28 ± 1.11	0.38	0.19 ± 0.02	11.80 ± 1.21	0.44
2.7	0.21 ± 0.02	8.59 ± 0.77	0.33	0.16 ± 0.01	16.41 ± 1.00	0.39	0.19 ± 0.02	11.89 ± 1.18	0.45
2.8	0.21 ± 0.02	8.69 ± 0.83	0.33	0.16 ± 0.01	16.53 ± 0.97	0.39	0.19 ± 0.02	12.02 ± 1.21	0.45
2.9	0.21 ± 0.02	8.87 ± 0.95	0.34	0.16 ± 0.01	16.62 ± 0.94	0.40	0.19 ± 0.02	12.08 ± 1.11	0.45
3	0.21 ± 0.02	9.03 ± 1.06	0.35	0.16 ± 0.01	16.83 ± 0.71	0.41	0.19 ± 0.02	12.26 ± 1.13	0.46

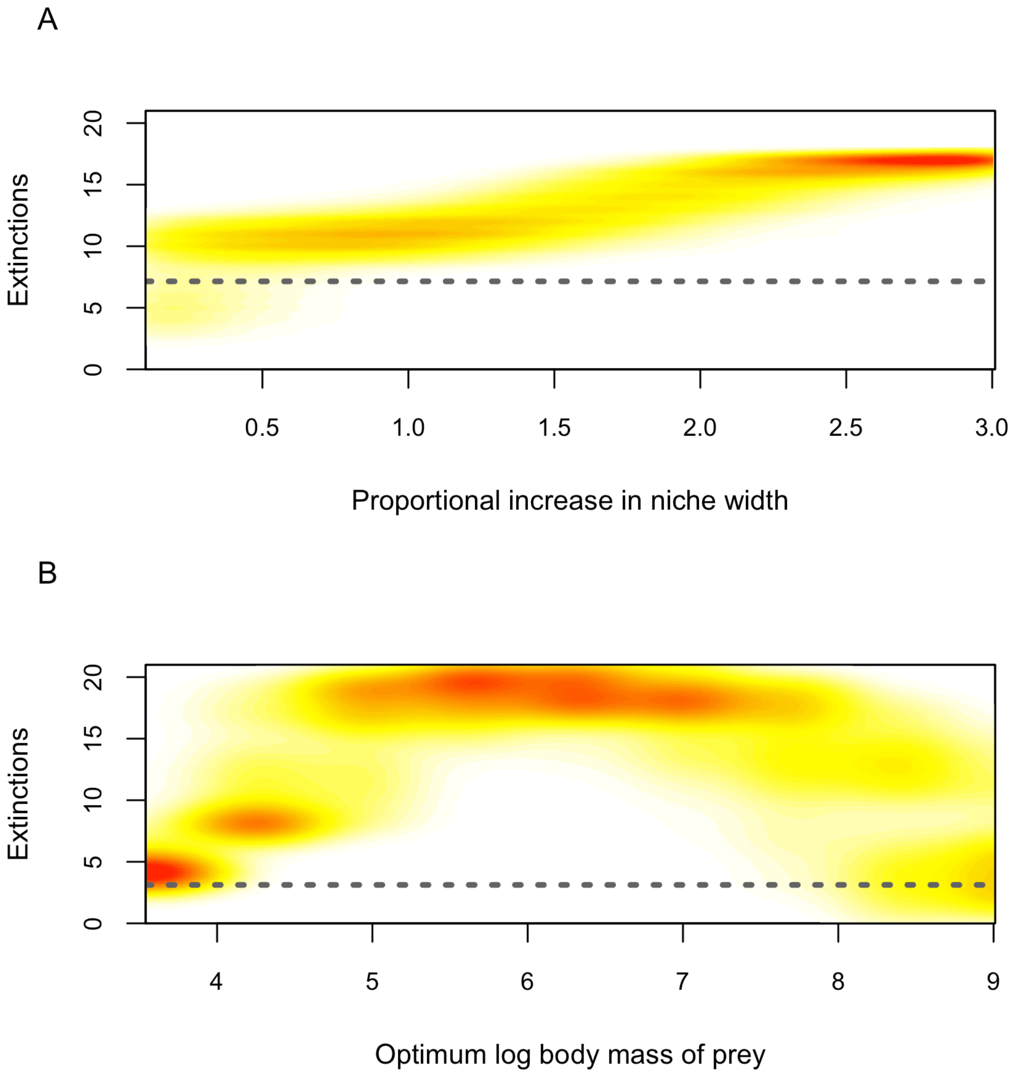

Figure S1. Number of extinctions under different scenarios. **A** shows the number of extinctions in simulations where we increased the niche width of prey species, but competition was twice as large as that in baseline simulations. **B** shows how the number of extinctions varies for simulations with humans targeting prey of different sizes. Colors portray the density of points considering 10^3 simulations under each scenario. The gray dotted line shows the average number of extinctions in 10^3 baseline simulations.

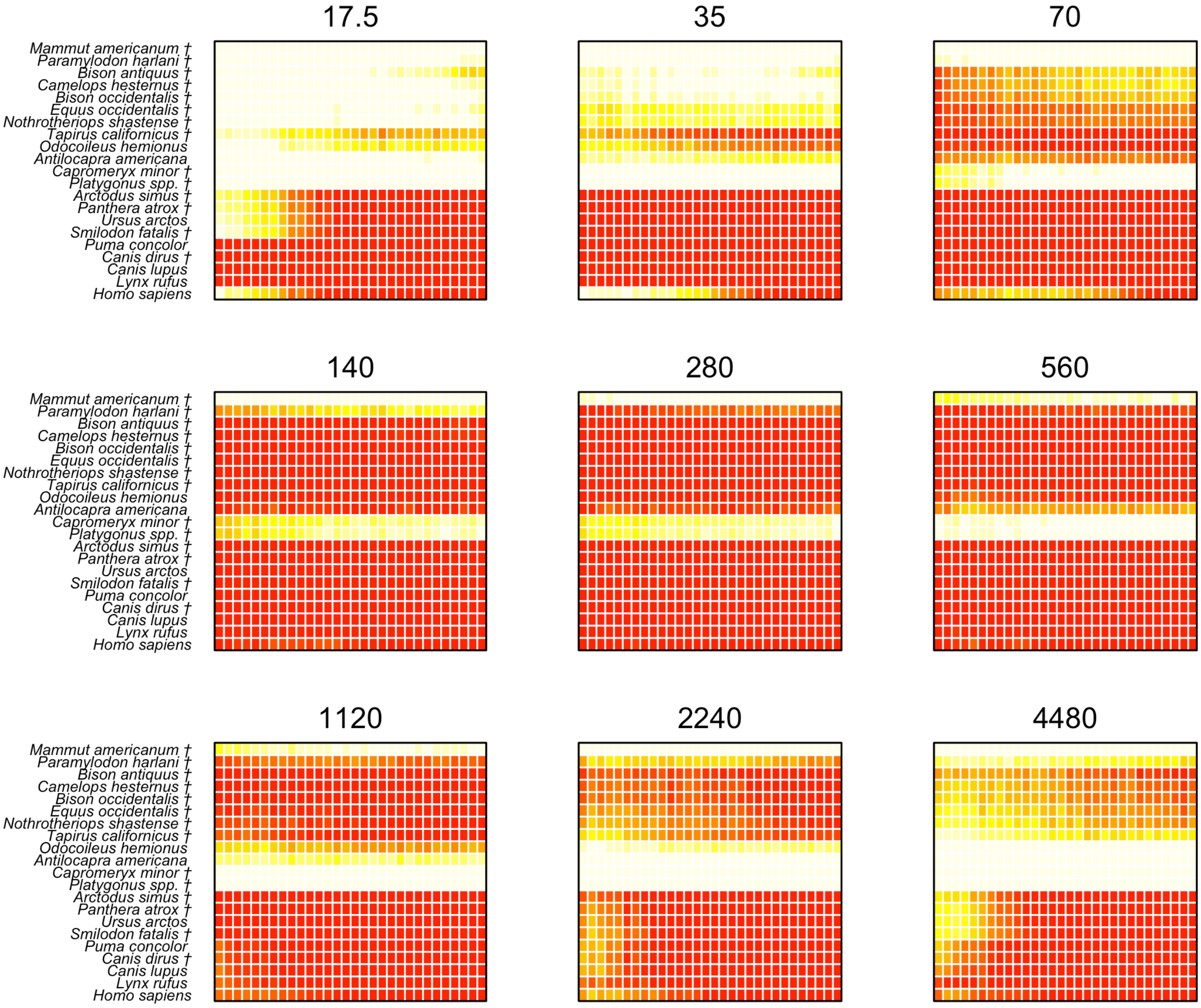

Figure S2. Probability of extinction of each species when combining the simulated effect of climate change (increasing niche widths) and human arrival. Each panel depicts how the probability of extinction varies with increasing niche width under each scenario of human hunting behavior (optimum prey size ranging from 17.5 kg to 4480 kg; above each panel). † signals extinct species.

SEÇÃO III

Consequências da extinção do Pleistoceno

CAPÍTULO 6

RECONSTRUCTING PAST ECOLOGICAL NETWORKS: THE RECONFIGURATION OF SEED-DISPERSAL INTERACTIONS AFTER MEGAFAUNAL EXTINCTION

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Abstract. The worldwide extinction of Pleistocene megafauna impacted ecological communities, affecting keystone ecological processes such as seed dispersal by vertebrates. Seed-dispersal interactions form networks, the structures of which have implications for community dynamics. Here, we combined ecological and paleontological data and network analyses to investigate how the structure of a species-rich seed-dispersal network in Central Brazil could have changed from the Pleistocene to the present and examine the possible consequences of such changes. Our results suggest the Pleistocene seed-dispersal network would be organized into modules similarly to the modern network. The episode of megafaunal extinction and the arrival of humans changed how seed dispersers were distributed among modules. The introduction of livestock partially restored the original network organization, but now introduced species and smaller native mammals are key components for the structure of the modern seed-dispersal network. We hypothesize the ongoing extinction of key large vertebrates will lead to the omnipresence of rearranged ecological networks most certainly affecting ecological processes.

INTRODUCTION

The species in a community form a network of interactions whose structure has implications for the ecological and evolutionary dynamics of the populations (Dunne 2006). Although snapshots in time are required to assess the structure of the community, ecological communities are constantly losing and gaining species through extinctions and invasions, thus network structure is continuously changing (Petanidou *et al.* 2008). Insight into how changes in species composition induce changes in the structure of ecological networks has been provided by studies focusing on the consequences of extinctions and the impact of species invasions (Memmott *et al*. 2004; Vilà *et al*. 2009). Extinction simulations have shown that food webs and mutualistic networks are highly robust to random extinctions (Dunne *et al*. 2002; Memmott *et al*. 2004). Similarly, studies on the effects of species invasions and on the temporal reconfigurations of ecological networks, in which species were both lost and gained over time, agree that the overall structure of networks is robust to changes in species composition (Petanidou *et al.* 2008; Vilà *et al.* 2009). Nonetheless, when a great number of species is lost, major changes in network structure and, consequently in network dynamics are expected.

The disruption of ecological networks is the most likely outcome of large extinction events in which many species are removed from the community within a relatively short time. A representative example of a large extinction event affecting community structure and function is the worldwide extinction of mammalian megafauna (body mass ≥ 44 kg) close to the Pleistocene-Holocene transition (the late Quaternary extinction, LQE; Martin & Klein 1984). Only in South America approximately 50 genera of large-bodied mammals went extinct (Koch & Barnosky 2006; Barnosky & Lindsey 2010). Although many studies have focused on the causes underlying the LQE (Koch & Barnosky 2006), the consequences of megafaunal extinctions have received considerably less attention (Galetti 2004; Rule *et al.* 2012).

There is compelling evidence that the large mammals that died out in the LQE were key species in the communities of which they were part (Martin & Klein 1984; Janzen 1986; Gill *et al.* 2009; Johnson 2009). Evidence supporting this view is represented by seed-dispersal anachronisms, whereby many extant plant species show traits that are best explained as having been shaped by interactions with extinct megafauna (Janzen & Martin 1982; Donatti *et al.* 2007; Guimarães *et al.* 2008). Indeed, anachronistic seed-dispersal systems are thought to be the result of the disruption of the seed-dispersal services formerly provided by megafauna due to the LQE (Janzen & Martin 1982; Guimarães *et al.* 2008). Those plant species probably suffered some degree of seed dispersal limitation after the extinction of their large seed dispersers (Janzen 1986), currently relying upon seed dispersal by scatter-hoarding rodents, surrogate megafauna (e.g., livestock), runoff, flooding, gravity, and human-mediated dispersal (Guimarães *et al*. 2008; Jansen *et al*. 2012). The study of how seed dispersal systems were affected by megafaunal extinction may allow us to understand how on-going defaunation will affect ecological processes.

Here, we examine the potential changes caused by the extinction of megafauna and following key historical events, such as the arrival of humans in the Americas and the introduction of exotic species (livestock and feral pigs) on a seed-dispersal network. We performed addition and removal simulations of extinct Pleistocene mammals, humans, and livestock in one of the most diverse seed-dispersal networks recorded to date, which includes species from major taxonomic groups of seed dispersers – mammals, birds, fish and reptiles – and the plants they interact with in the Pantanal (Donatti *et al.* 2011). First, we compiled from the literature a list of mammalian megafauna likely to occur in the Pantanal during the Pleistocene. Second, we combined data on the feeding ecology of Pleistocene megafauna (e.g., MacFadden & Shockey 1997; MacFadden 2000) and information on seed-dispersal anachronisms (Guimarães *et al*. 2008) to outline the putative interactions among the extinct megafauna and fleshy-fruited plants. Finally, we built a potential network time series from the end of the Pleistocene to the present day and used metrics that describe the network organization to evaluate the changes in the patterns of interactions between seed dispersers and plants over time. Because the LQE represented a major change in the composition of mammalian assemblages (Martin & Klein 1984), we expected that network organization in the Pleistocene would be substantially different and would have suffered a great reconfiguration after most large-bodied mammals became extinct. To our knowledge, this is the first attempt to reconstruct how a large extinction event and human arrival reconfigures an ecological network.

METHODS

Study site

The seed-dispersal interactions were surveyed in two neighboring locations in the Brazilian Pantanal: Rio Negro (19°34'15'' S 56°14'43'' W) and Barranco Alto farms (19°34'40'' S 56°09'08'' W), covering 7500 ha and 11 000 ha, respectively (Donatti *et al.* 2011). The vegetation in these locations is characterized by gallery forests, savannas, and semi-deciduous forests. As in all the South America lowlands (Bush *et al*. 2011), paleoclimatic studies suggest that the Pantanal experienced climatic fluctuations during the Late Pleistocene and Holocene (Assine & Soares 2004) that resulted in vegetation shifts (Whitney *et al.* 2011). Although such changes most certainly affected plant communities, palynological data shows that by 19.5 kyr BP, when tropical forest communities began to expand following the Late Glacial Maximum (LGM), most plant taxa represented in the modern pollen assemblages were already present in the Pantanal region (Whitney *et al.* 2011). Therefore, even considering that the relative plant abundances likely changed during the interval considered here, changes in species occurrence in this particular region seem to have been less pronounced. For this reason, in our baseline analysis, we assume the plant taxa were the same throughout the time series. However, we also performed simulations to explore the effects of changes in plant composition on the network organization (see below).

Pleistocene mammals

Several sites containing fossils of Pleistocene mammals can be found within 200 km of the study sites (Scheffler *et al.* 2010). We assume that the species found in those sites could also be found in the study sites due to the high mobility of megafaunal species and the vegetational, climatic and topographic homogeneity of the Pantanal floodplain. Fossil data for extinct megafaunal assemblages originate from limestone caves of the Serra da Bodoquena (19°48'-22°16'S; 56°32'-57°24'W), Brazil (Salles *et al*. 2006; Scheffler *et al*. 2010). Although dates for the fossils are unavailable, fossils are from taxa that survived into late Pleistocene (Barnosky & Lindsey 2010). The estimated body masses were obtained from literature (Smith *et al.* 2003; Table S1). Dietary data were compiled from feeding ecology studies of each taxon (Table S1). When estimated body mass or diet of a given species was not available, we used information on closely related taxa.

Archeological evidence suggests that fruits were also important in the diet of paleoindians in the Neotropics (Roosevelt *et al.* 1996). In fact, seed dispersal by humans that live in traditional communities close to forested areas seems to be important for several plant species in the tropical region (Guix 2009). To incorporate the role of paleoindians as seed dispersers, we assigned interactions to humans while assuming that the fruits used were the same as those used currently by the indigenous people that inhabit the Pantanal region (Pott *et al.* 2011). This assumption is supported by the fact that fruits of several species have evidence of long-term use by indigenous people, such as some palm fruits.

The network time series

We used the seed-dispersal network sampled by Donatti *et al.* (2011). This dataset contains only seed-dispersal interactions; fruit consumption by seed predators or non-disperser pulp consumers was not included in the assembly of the network. We included seed dispersal by introduced species, such as cattle and feral pigs, which interact with several plant species in the area (Galetti, M. unp. data; Donatti *et al.* 2007).

To evaluate the possible structural differences in the Pantanal seed-dispersal network over time, we built a potential network time series from the Pleistocene to the present. We modeled four key periods in network reorganization: (i) the plant-frugivore network in the late Pleistocene, after the expansion of tropical forest communities that followed the LGM (Whitney *et al.* 2011); (ii) the early Holocene network in which most megafaunal species died out and paleoindians already inhabited the region; (iii) the Colonial period (1800's), with the onset of livestock production in the Pantanal region (Abreu *et al.* 2010), with cattle, pigs, and also indigenous people acting as dispersers; and (iv) the modern period in which humans are no longer relevant dispersers due to the demise of local human communities but cattle and pigs are part of the seed-disperser assemblage (Fig. 1). For simplicity, we assume that the extant species interacted with the same plant species in the past, an assumption supported by some degree of niche conservatism in the identity of mutualistic partners observed in seed-dispersal networks (Rezende *et al.* 2007).

Although we included extant grazers (e.g., cattle) in some of the seed-dispersal networks, to reconstruct the Pleistocene network, we opted for a conservative approach and included only those mammals with browsing and mixed diets, i.e., those taxa more likely to have fruits as an important component on their diets (MacFadden & Shockey 1997; Table S1). By doing so we attempted to avoid overestimating the role of Pleistocene megafauna. To define the interactions that megafaunal species potentially established in seed-dispersal networks, we identified fruits showing characteristics that fit the megafaunal syndrome, i.e., similar to fruits that are dispersed by the extant megafauna in Asia and Africa (Guimarães *et al*. 2008). Megafaunal fruits are characterized by a large size (diameter >4 cm) and contain extremely large (diameter >2 cm) individual seeds (type I fruits), or by extremely large fruits (diameter >10 cm) that contain a large number of moderate- or small-sized seeds (type II fruits; Guimarães *et al*. 2008). We assume that the extant plant species with fruits that possess those characteristics interacted more frequently with the megafauna in the past than did other extant plant taxa. Although megafauna may have interacted with other types of fruits (Janzen & Martin 1982; Janzen 1984), by restricting megafaunal interactions to those plants and fitting an operational and conservative definition of megafaunal fruits (Guimarães *et al*. 2008), we avoid overestimating the structural effects of megafaunal extinction. However, as restricting megafaunal interactions to a subset of plant species certainly affects the network topology, we performed additional simulations to test how our results are affected if we consider the consumption of non-megafaunal fruits by the extinct megafauna (see below).

Network structure

For each of the reconstructed networks, we analyzed the two most commonly explored structural patterns of mutualistic networks: nestedness (Bascompte *et al.* 2003) and modularity (Olesen *et al.* 2007). Nestedness occurs if the interacting assemblage of a species is a subset of the interacting assemblage of species with more interactions (Bascompte *et al.* 2003). We used the index *NODF* (Almeida-Neto *et al.* 2008) to compute the degree of nestedness of each network. *NODF* ranges from 0, when the matrix is non-nested, to 100, when the matrix is perfectly nested. The modules within an ecological network are subsets of species that are more connected to each other than to other species in the network (Olesen *et al.* 2007). We detected modules using the simulated annealing algorithm to maximize the index of modularity M (Guimerà & Amaral 2005). M equals 0 if species are placed at random into modules and approaches 1 if there are few between-module interactions. Although M does not take into account the fact that seed-dispersal networks are two-mode networks, it is also suited to estimate modularity of two-mode networks (Olesen *et al.* 2007). Moreover, because the theoretical model we used to test the significance of M (see below) also yields two-mode networks, any difference in M among real and theoretical networks cannot be related to the two-mode structure (Pires *et al.* 2011).

To verify the significance of the empirical degrees of nestedness and modularity of each network, we used a null model approach. We generated 10^3 theoretical networks in which the probability that an animal species, i, interacts with a plant species, j, is

$$P(r_{ij} = 1) = \frac{1}{2}\left(\frac{k_i}{P} + \frac{k_j}{A}\right)$$

in which k_i is the number of plants that interact with the animal species i, k_j is the number of animal species that interact with plant species j, P is the plant species richness and A is the animal species richness (Bascompte *et al.* 2003). *NODF* and *M* were then computed for each theoretical network to generate null distributions of *NODF* and *M* values.

We also evaluated how the role of a species in the network structure would differ between Pleistocene and modern networks. We assigned a role for each species in the network based on the number of its interactions with species within its own module (z) and on how evenly distributed its interactions are across species in different modules (c; Guimerà & Amaral 2005). Species with low z and low c values are peripheral species interacting with species within their own module. Species with either a high z or c were generalists and either (1) module hubs, i.e., highly connected within their own module (high z and low c), or (2) connectors, those species that link modules (low z and high c; Olesen *et al.* 2007).

Megafauna feeding on non-megafaunal fruits

In our baseline analysis we assumed that megafauna would interact with the same subset of available fruits, which results in total overlap of interaction patterns. This overlap may impact network structure in non-obvious ways. For instance, megafaunal species could form an additional module with the megafaunal fruits, increasing modularity. Alternatively, if megafaunal fruits are in different modules in the modern network, adding several species with a similar interaction pattern could merge such modules, reducing modularity. Nevertheless, it is unlikely that all megafaunal species fed on the exactly same set of species. Thus, we performed an analysis to test if the degree of modularity and module assignment in the Pleistocene network (time period I) would be different if megafaunal species varied in their fruit consumption. In this second set of simulations we assume megafaunal species would feed, in addition to megafaunal fruits, on a variable set of non-megafaunal fruit species (Appendix S1).

Effects of shifts in plant composition

Even though palynological data support our assumption that the floristic composition in the region was reasonably similar between the Pleistocene and today (see Study site), we performed an additional analysis to test whether our results were robust when this assumption was relaxed (Appendix S2). We performed random removals of the plants in the Pleistocene seed-dispersal network and computed modularity for each network registering the module each seed disperser was assigned to. If the modular organization were highly sensitive to changes in the plant composition we should expect that removing any small proportion of plants would result in a very different modular organization

RESULTS

We identified nine species of Pleistocene large herbivores that lived close to the area assessed by Donatti *et al.* (2011). Five of these nine species were mixed-feeders or browsers (Table S1) and thus more likely to be relevant seed dispersers. Ten of the 48 plant species in the modern network (20.8%) are plants with fruits that fit the megafaunal seed-dispersal syndrome (Table S2).

All the networks in the time series were both more nested and more modular than expected by the null model (Table 1). However, the number and composition of the modules changed across networks (Table S2). The Pleistocene network was best characterized by five modules (Fig. 1). Two modules are dominated by bird species, with large birds, such as toucans and guans, being more frequent in the first bird-dominated module (average body mass ± SD = 0.24 ± 0.07 kg) and small birds, mainly passerine birds, in the second (0.06 ± 0.01 kg). Mammals also dominate two modules: one of these mammal-dominated modules included mainly large mammals ($1.6\times10^3 \pm 2.2\times10^3$ kg), whereas small mammals dominated the second (35.19 ± 69.09 kg). The module dominated by large mammals would include mainly the Pleistocene megafauna and one small mammal, the agouti (genus *Dasyprocta*), scatter-hoarding rodents that feed upon and disperse large seeds (Jansen *et al.* 2012). The second mammal-dominated module would include mammals that are small-bodied compared to the Pleistocene megafauna, such as peccaries (*Pecari* and *Tayassu* spp.) and the coati (*Nasua nasua*). If we relax the assumption that megafauna only interacted with megafauna-dependent fruits, the predicted degree of modularity of the Pleistocene networks should be smaller (M = 0.368 ± 0.006). Nevertheless, the module organization of the two mammal-dominated modules is consistent even when considering that megafauna would have interacted with several other plant species that do not fit the megafaunal dispersal syndrome (Appendix S1 and Table S3). The two mammal-dominated modules and the module dominated by large birds were also robust after relaxing the assumption that the Pleistocene and modern plant assemblages were similar (Appendix S2 and Fig. S1).

Table 1. Nestedness (*NODF*) and modularity (*M*) of the seed dispersal networks representing each time period in the time series and the average nestedness ($NODF_R$) and modularity (M_R), ± standard deviation, for their randomized counterparts.

	Time period			
	I [Megafauna]	II [Humans]	III [Livestock]	IV [Modern]
NODF	27.45	31.88	32.09	29.46
$NODF_R$	19.73 ± 1.40	20.50 ± 1.18	25.34 ± 1.21	20.59 ± 1.12
M	0.45	0.39	0.37	0.39
M_R	0.33 ± 0.01	0.33 ± 0.01	0.31 ± 0.01	0.33 ± 0.01

In the second major period, in the early Holocene, after the Pleistocene megafaunal extinction, paleoindians, by interacting with a considerable proportion of the plant species, would have changed the module organization of the network, merging both mammal-dominated modules into a single module (Fig. 1). Conversely, the arrival of livestock (pigs and cows) in the third period (Colonial period) would have restored the large/small mammal modules. Finally, in the modern time period, a time when humans are no longer relevant as dispersers, but cows and pigs still act as seed dispersers, the network is, again, best characterized by the five modules (Fig. 1).

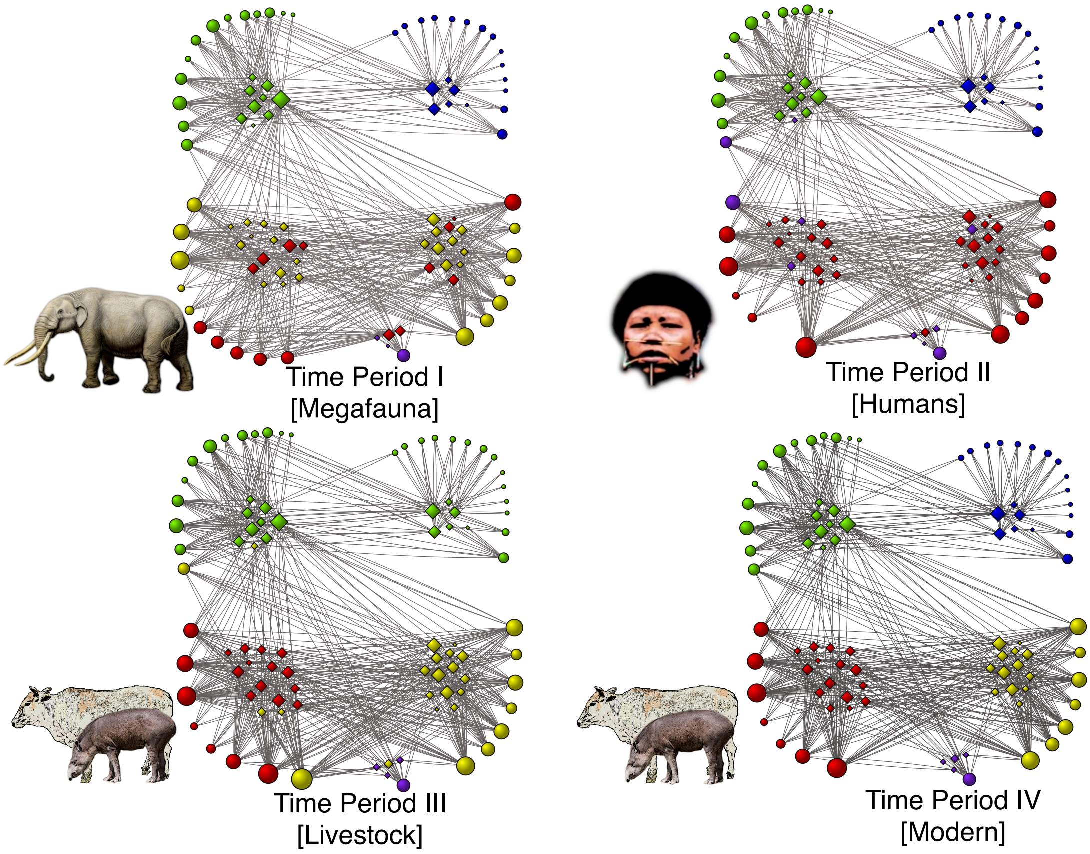

Figure 1. Seed-dispersal networks representing each time period in the network time series. Nodes represent animals (circles) and plants (diamonds) and the size of a node is proportional to its number of interactions. Colors identify the modules each species was assigned to. Green and blue modules are dominated by large and small birds, respectively; red and yellow modules are dominated by large and small mammals; the purple module is defined by a fish species (*Piaractus mesopotamicus*). In all networks species occupy the same position defined for the modern network, even when assigned to different modules, to allow comparisons. When the color of a given node changes from one network to the other, that species was assigned to different modules in different periods. Representative species within the module dominated by large mammals are represented by illustrations to highlight the changes across time periods. See Table S2 for the species composition of each module.

The changes in mammal-dominated modules across the time series had consequences for the interaction patterns of the plants in those modules. In the late Pleistocene, the members of the large mammal module would be mainly the Pleistocene megafaunal species weighing in the order of 10^3 kg. In contrast, most extant mammals that comprise the module in the modern network, such as the tapir (*Tapirus terrestris*), black howler (*Alouatta caraya*), and coati (*Nasua nasua*), would be, functionally, small mammals in the Pleistocene network (Fig. 1 and Table S2). As a result, if we compare the two extremes of the time series, the Pleistocene and modern networks, major differences with regard to the distribution of the body mass of dispersers are noted. In the Pleistocene network, plants within the large mammal-dominated module would have dispersers that are, on average, much larger than in the modern network (Fig. 2). However, as the network diminished to its current size, so did the dispersers, and the plants in both mammal-dominated modules now have seed dispersers of a similar size (Fig. 2).

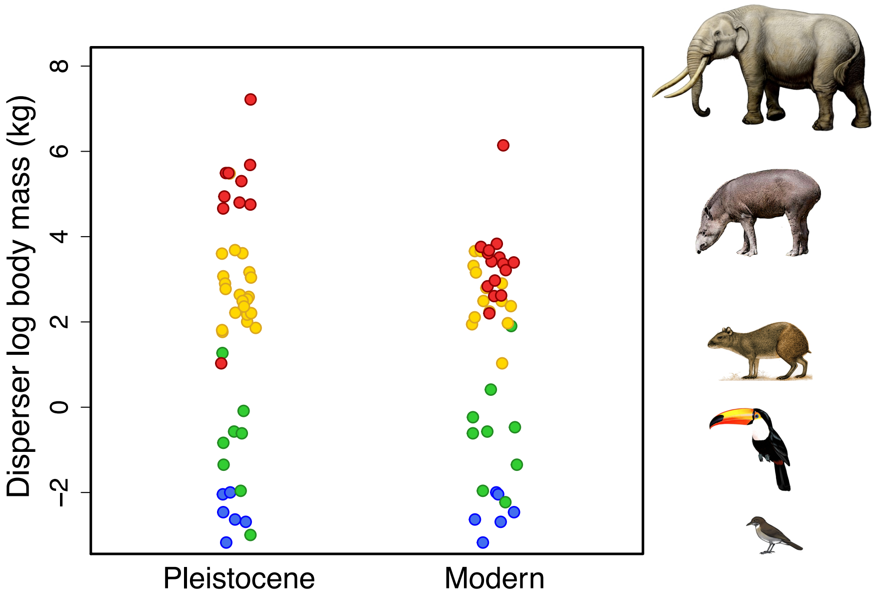

Figure 2. Average body size of dispersers of each plant species in the Pleistocene and modern seed dispersal networks. Colors indicate the module each plant species was assigned: red = large mammal-dominated module, yellow = small mammal-dominated module, green = large bird-dominated module, and blue = small bird-dominated model.

Because of the modular organization, the effects of megafauna loss mainly influenced the plant species within the mammal-dominated modules, whereas the average size of dispersers of plants in the bird-dominated modules would be similar across both periods (Fig. 2). This is also true for the functional roles of species. We found that nearly all of the species that differ in their contribution to the connections within and between modules were species assigned to the mammal-dominated modules in the modern network (Fig. 3). Most of these species, such as the crab-eating fox (*Cerdocyon thous*), the red brocket deer (*Mazama americana*), and the tapir (*Tapirus terrestris*), have larger *c*-values in the modern network, indicating that they are now more relevant as module connectors and are thus more central in the modern network, than in the Pleistocene network. Conversely, other mammal species, such as the white-lipped peccary (*Tayassu pecari*), the collared peccary (*Pecari tajacu*) and the agouti (*Dasyprocta* sp.), have larger *z*-values in the modern network, indicating they are more central to their module in the modern period than they would have been in the Pleistocene (Fig. 3).

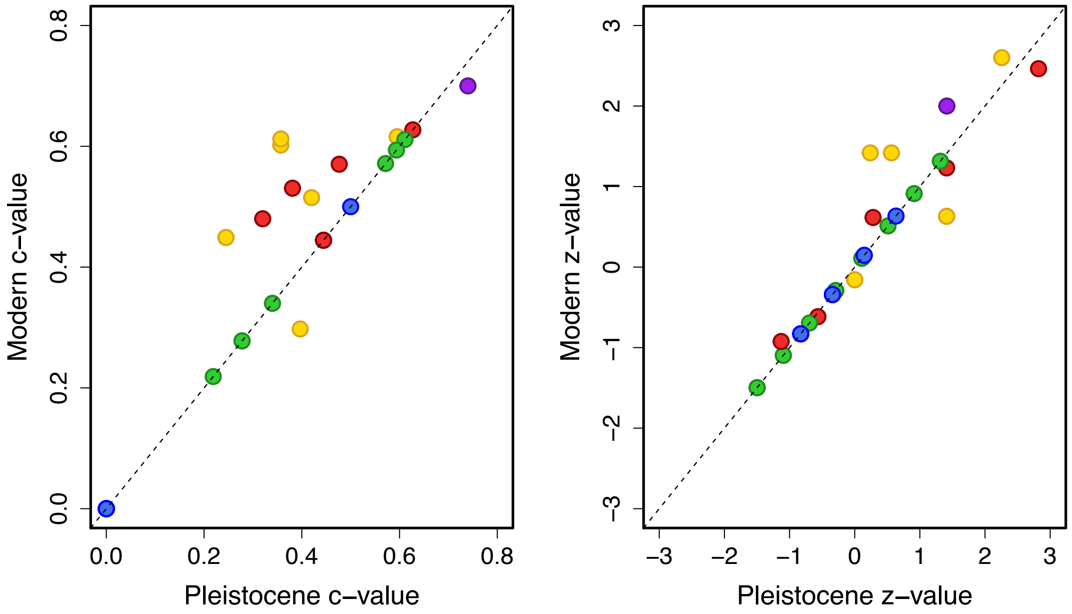

Figure 3. Network roles of extant species in the modern and Pleistocene seed-dispersal networks. The metric *c* measures the inter-module connectivity, and *z* measures intra-module connectivity. Colors indicate the modules each species is assigned to in the modern network (following the color scheme of figures 1 and 2). Points that fall outside the 1/1 line represent those species whose role changed from the Pleistocene to the modern network.

DISCUSSION

Many of the large mammals that became extinct in South America during the Pleistocene were also potential seed dispersers of extant plant species (Janzen & Martin 1982; Guimarães *et al.* 2008). The approach we used here, albeit conservative, suggests that the demise of the megafauna could have had important consequences for the organization of the seed-dispersal network in the Pantanal region. The Pleistocene network, which was most likely characterized by two modules of mammalian seed dispersers, was reconfigured after the loss of most of the large-bodied mammals in the LQE. Acting as generalist foragers, humans would have rearranged the seed-dispersal network in a novel way, merging together the two modules dominated by mammals. The organization of the Pleistocene network would have been partially restored after the arrival of pigs and cattle, which consume the fruits, potentially dispersing the seeds, of many of the plants presumably dispersed by Pleistocene megafauna (Janzen & Martin 1982; Donatti *et al.* 2011).

The introduction of surrogate seed dispersers, that is, extant species ecologically equivalent to the extinct species ("rewilding"; Donlan *et al.* 2006), has been suggested as a management tool to locally restore ecological and evolutionary processes in those areas where large vertebrates died out (Donlan *et al.* 2006; Griffiths *et al.* 2011). Although our results suggest livestock could have partially restored the structural properties of the Pantanal seed-dispersal network, whether or not livestock is able to compensate for the loss of extinct megafauna within the community remains to be tested.

Pleistocene and modern networks with surrogate Pleistocene dispersers would still be very dissimilar in at least one key feature: the body size range of the extant seed dispersers is truncated at the large end of the size spectrum. This difference in the body sizes of seed dispersers has a number of implications for seed dispersal. Large frugivores are the main seed dispersers of seeds that are too large for smaller mammals and birds (Janzen & Martin 1982; Hansen & Galetti 2009), and are more likely to promote long-distance dispersal, connecting plant populations across fragmented landscapes (Nathan & Muller-Landau 2000; Fragoso *et al.* 2003). Also, because large mammals ingest more seeds per feeding event, seeds are more likely to be dispersed in clumps, potentially affecting seed germination success and the spatial distribution of the adult plants (Fragoso *et al*. 2003). Therefore, the extinction of megafauna is likely to have affected population dynamics, the patterns of spatial distribution and the genetic structure of large-seeded plants in ways that livestock may not compensate.

Our results also indicate how far-reaching the impacts of megafaunal extinction, for other plants and seed dispersers, could have been. In a modular system, species are tightly connected to other species in the same module but loosely connected to the rest of the network. As a result, the direct effects of structural changes are often localized, directly impacting the species within certain modules instead of spreading to the entire network (Dunne 2006). As seed dispersal and the recruitment of plants that relied on megafaunal species decreased, however, those plants that are dispersed by other primary seed dispersers, such as birds, and by secondary dispersers, such as rodents, would face lower competition and higher probabilities of recruitment, leading to a positive indirect effect of the megafaunal extinction on plant species in other modules of the network. Palynological data suggest some fruiting tree species declined in abundance, whereas Cyperaceae and Poaceae increased, in the Pantanal region during late Pleistocene (Whitney *et al*. 2011). Although this vegetation shift is likely related to changes in climate conditions, the loss of megafauna might have contributed. A similar phenomenon has been reported for modern-day communities in South and Central America, where hunting has reduced the densities of large- and medium-sized seed dispersers, leading to an increase in the richness and densities of plants that are dispersed by small, non-game animals and by abiotic means (Wright *et al.* 2007). As better data on the composition of the plant communities in the past is obtained from the fossil record, future studies should be able to test whether a shift in plant composition followed the Pleistocene megafaunal extinction, thus contributing to our understanding of the large-scale consequences of defaunation both in the past and in modern times.

A further consequence of the LQE was the increase in the importance of extant species across time. The megafaunal plants now rely on dispersal by smaller species, such as the agouti (*Dasyprocta* spp.; Jansen *et al.* 2012), and only on a few large mammals, such as feral pigs and the tapir (Donatti *et al.* 2011). Our results suggest species such as the tapir, brocket deer, and peccaries would have had a more peripheral role in the seed-dispersal network during the Pleistocene when compared to modern communities. The same seems to be taking place in modern communities. As populations of Asian elephants and rhinos decline, large-seeded plants dispersed by them have to rely on smaller species such as the Asian tapir, which seems to be far less effective as seed disperser of large-seeded plants (Campos-Arceiz *et al.* 2012).

Our knowledge of the ecology of modern communities is biased toward systems that are already largely defaunated (Corlett 2013), but the roles that species play in the community could have been different in the past. The few extant large vertebrates in the tropical ecosystems are the last option for the seed dispersal of plant species that have lost a significant proportion of their interaction partners. The ongoing or future consequences of local extinctions of such large-bodied seed dispersers are likely to have deleterious effects for the plant species that now rely on them.

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APPENDICES

Appendix S1. Sensitivity of modules to the interaction patterns of Pleistocene megafauna

We performed an additional analysis to test whether the module organization we found for the Pleistocene network was sensitive to the way we assigned interactions to megafauna. To do that we relaxed our conservative assumption that Pleistocene megafauna only interacted with highly dependent megafauna fruits. Because in the modern network there is a strong positive relationship ($F_{40,1} = 73.61$, $R^2 = 0.64$; $p < 0.001$) between the number of interactions, k, of seed-dispersers and average body mass, m (Donatti *et al.* 2011), we first used the equation describing this linear relationship, $k = 8.27 + 1.71*\ln(m)$, to estimate the expected number of interactions for each megafauna species based on body mass. Most of those species weighted more than 10^3 kg and so, according to the k/m relationship, they should have around 20 interactions. Because only 10 out of the 45 plant species were identified as potential megafaunal plants, we generated an ensemble of 100 potential Pleistocene networks in which all megafaunal species interacted with the plants with megafaunal fruits, but their remaining interactions were randomly assigned to other plant species. By doing so, we randomly distributed more than 50% of the interactions of each megafaunal species. We then computed modularity for each network and registered the modules each seed disperser was assigned to. All reconstructed networks had three or four modules with an average modularity (±SD) of 0.368 (± 0.006). For all networks a module dominated by small mammals and one dominated by large mammals was identified. Even randomly distributing more than a half of the interactions of megafaunal species they were consistently assigned to the same module (Table S3). Approximately half of the networks also had two modules dominated by birds, whereas for the other half the two bird-modules were merged into one. However, when two bird-dominated modules were identified, small birds were consistently assigned to one module and larger birds to the other (Table S3). In Table S3 we report the frequency with which a given species was assigned to each module. These results show that even though, as expected, the degree of modularity is sensitive to the way interactions are assigned to megafauna, the module organization found for our more conservative assignment of megafaunal interactions, which is presented the main text, is robust.

Appendix S2. Sensitivity of modules to changes in vegetation

Although palynological data suggest the floristic composition during late Pleistocene in this region was similar to today's composition (Whitney *et al.* 2011), we performed an additional analysis to test whether the module assignment pattern we found for the Pleistocene network was robust to changes in the plant composition. We performed random removals of 10%, 20%, 30%,…90% (100 simulations each) of the plants in the Pleistocene seed-dispersal network, computed modularity for each network, and registered the module each seed disperser was assigned to. If the modular organization were highly sensitive to changes in the plant composition we should expect that removing any small proportion of plants would result in a very different modular organization. Our analysis suggests the module assignment pattern is highly robust. Removing plants sometimes resulted in seed dispersers loosing all their interaction patterns and thus not being assigned to any module. However, when assigned to a module, seed dispersers were often assigned to the same modules they were assigned to in the network containing all plant species. As in the analysis testing the effects of adding more interactions to Pleistocene megafauna (Appendix S1), the module dominated by small birds was indentified in approximately 50% of the simulations of each scenario. Yet, whenever two bird-dominated modules were identified, those species originally assigned to the module dominated by small birds were consistently grouped together in the same module. The modules dominated by large mammals, small mammals and large birds were robust to changes in the plant assemblage. Substantial changes in the module assignment patterns are only found after removing more than 50% of the plant species (Fig. S1), when, for instance, small mammals that were consistently grouped together are eventually assigned to the module originally dominated by small birds.

Table S1. Extinct megafaunal species, with estimated body mass and diet information, found in paleontological sites in Serra da Bodoquena, Brazil. Asterisks indicate the species that were included in the Pleistocene seed dispersal network.

Taxon	**Body Mass (kg)**	**Diet**
Artiodactyla		
*Palaeolama major**	1,000	Browser (MacFadden and Shockey 1997)
Cingulata		
Glyptodon sp.	1,430	Grazer to mixed-feeder (MacFadden 2000)
Pampatherium sp.	150	Grazer (de Iuliis, Bargo and Vizcaíno 2000)
Litopterna		
Xenorhinotherium sp.*	980	Browser (MacFadden and Shockey 1997)
Notoungulata		
Toxodon platensis	1,600	Grazer (Macfadden *et al*. 1994)
Perissodactyla		
Equus sp.	350	Grazer (Macfadden *et al*. 1994)
Pilosa		
*Eremotherium laurillardi**	800	Browser (Bargo 2001)
*Glossotherium lettsomi**	1,000	Mixed-feeder (Bargo 2001)
Proboscidea		
*Stegomastodon waringi**	6,000	Mixed-feeder to browser (Prado *et al*. 2005)

Table S2. Module assignment of each species within the seed-dispersal network for each time period. LM = large mammal-dominated module; SM = small mammal-dominated module; LB = large bird dominated-module; SB = small bird-dominated module; F = fish module. Pleistocene megafaunal species and megafaunal fruits are identified with an asterisk (*)

	Time period			
	I [Pleistocene]	II [Humans]	III [Livestock]	IV [Modern]
Animals				
Casiornis rufa	SB	SB	LB	SB
Columbina talpacoti	LB	LB	LB	LB
Crax fasciolata	SM	SM	SM	SM
Cyanocorax chrysops	SB	SB	LB	SB
Cyanocorax cyanomelas	LB	LB	LB	LB
Gnorimopsar chopi	LB	LB	LB	LB
Guira guira	LB	LB	LB	LB
Icterus croconotus	SB	SB	LB	SB
Myiarchus ferox	SB	SB	LB	SB
Myiodynastes maculatus	SB	SB	LB	SB
Ortalis canicollis	LB	LB	LB	LB
Paroaria coronata	SB	SB	LB	SB
Pipile jacutinga	LB	LB	LB	LB
Pitangus sulphuratus	SB	SB	LB	SB
Psarocolius decumanus	LB	LB	LB	LB
Pteroglossus castanotis	LB	LB	LB	LB
Ramphastos toco	LB	LB	LB	LB
Ramphocelus carbo	LB	LB	LB	LB
Rhea americana	LM	F	LB	LM
Saltator coerulescens	SB	SB	LB	SB
Tachyphonus rufus	LB	LB	LB	LB
Thraupis palmarum	SB	SB	LB	SB
Thraupis sayaca	SB	SB	LB	SB
Trogon curucui	SB	SB	LB	SB
Turdus rufiventris	SB	SB	LB	SB
Turdus sp.	LB	LB	LB	LB
Tyrannus melancholicus	SB	SB	LB	SB
Tityra cayana	SB	SB	LB	SB
Alouatta caraya	SM	LM	LM	LM
Cerdocyon thous	SM	LM	SM	SM
Dasyprocta sp.	LM	LM	SM	SM
Mazama americana	SM	LM	SM	SM
Nasua nasua	SM	LM	LM	LM
Pecari tajacu	SM	LM	SM	SM

Procyon cancrivorus	SM	LM	LM	LM
Tapirus terrestris	SM	LM	LM	LM
Tayassu pecari	SM	LM	SM	SM
Geochelone carbonaria	SM	LM	SM	SM
Piaractus mesopotamicus	F	F	F	F
Artibeus sp.	LB	F	SM	SM
Sus scrofa	—	—	LM	LM
Cattle	—	—	LM	LM
Humans	—	LM	SM	—
*Eremotherium laurillardi**	LM	—	—	—
*Stegomastodon waringi**	LM	—	—	—
*Glossotherium lettsomi**	LM	—	—	—
Xenorhinotherium sp.*	LM	—	—	—
*Palaeolama major**	LM	—	—	—
Plants				
Acrocomia aculeata (Arecaceae)*	LM	LM	LM	LM
Agonandra brasiliensis (Opiliaceae)	SM	LM	LM	LM
Alibertia sessilis (Rubiaceae)	SM	LM	SM	SM
Annona dioica (Annonaceae)	SM	LM	SM	SM
Attalea phalerata (Arecaceae)*	LM	LM	LM	LM
Attalea speciosa (Arecaceae)*	LM	LM	LM	LM
Bactris glaucescens (Arecaceae)	SM	F	LM	LM
Byrsonima orbignyana (Malpighiaceae)	SM	LM	SM	SM
Byrsonima verbascifolia (Malpighiaceae)	SM	LM	SM	LM
Caryocar brasiliensis (Caryocaraceae)*	LM	LM	SM	SM
Cecropia pachystachya (Urticaceae)	LB	LB	LB	LB
Copernicia alba (Arecaceae)	LB	LB	LB	LB
Couepia uiti (Chrysobalanaceae)	SM	LM	LM	LM
Curatella americana (Dilleniaceae)	LB	LB	LB	LB

Diospyros hispida (Ebenaceae)	SM	LM	LM	LM
Dipteryx alata (Fabaceae)*	LM	F	LM	LM
Doliocarpus dentatus (Dilleniaceae)	SB	SB	LB	SB
Dulacia egleri (Olacaceae)	LM	LM	SM	SM
Enterolobium contortisiliquum (Fabaceae)*	LM	LM	SM	SM
Eugenia dysenterica (Myrtaceae)	SM	LM	SM	SM
Ficus gomelleira (Moraceae)	SM	F	SM	SM
Ficus pertusa (Moraceae)	LB	LB	LB	LB
Garcinia brasiliensis (Clusiaceae)	SM	LM	LM	LM
Genipa americana (Rubiaceae)*	LB	LB	LB	LB
Guazuma ulmifolia (Malvaceae)	SM	LM	SM	SM
Hancornia speciosa (Apocynaceae)	SM	LM	SM	SM
Hymenaea stigonocarpa (Fabaceae)*	LM	LM	SM	SM
Inga laurina (Fabaceae)*	LM	F	F	F
Licania parvifolia (Chrysobalanaceae)	F	F	F	F
Melicoccus lepidopetalus (Sapindaceae)	SM	LM	LM	LM
Mouriri elliptica (Melastomataceae)	SM	LM	SM	SM
Ocotea dyospirifolia (Lauraceae)	SB	SB	LB	SB
Pouteria gardneri (Sapotaceae)	SM	LM	LM	LM
Pouteria ramiflora (Sapotaceae)	SM	LM	SM	LM
Protium heptaphyllum (Burseraceae)	LB	LB	LB	LB
Psidium nutans (Myrtaceae)	SM	LM	SM	SM
Psittacanthus caliculatus (Loranthaceae)	SB	SB	LB	SB
Psittacanthus cordatus (Loranthaceae)	SB	SB	LB	SB
Rhamnidium elaeocarpum	LB	LB	LB	LB

(Rhamnaceae)				
Salacia elliptica (Celastraceae)*	LM	LM	SM	F
Sapindus saponaria (Sapindaceae)	LB	F	SM	LB
Sterculia apetala (Malvaceae)	LB	LB	LB	LB
Solanum viarum (Solanaceae)	SM	LM	LM	LM
Swartzia jorori (Fabaceae)	SB	SB	LB	SB
Syagrus flexuosa (Arecaceae)	SM	LM	LM	LM
Tocoyena formosa (Rubiaceae)	F	F	F	F
Vitex cymosa (Verbenaceae)	SM	LM	LM	LM
Zanthoxylum rigidum (Rutaceae)	SB	SB	LB	SB

Table S3. Module assignment when considering interactions with non-megafaunal fruits. Relative frequency (in 100 networks) with which a given species (rows) was assigned to each module (columns) after considering the potential interactions of Pleistocene megafauna with non-megafaunal fruits (Appendix S1). Pleistocene megafauna are identified with an asterisk (*)

	Large mammals	**Small mammals**	**Large birds**	**Small birds**
Casiornis rufa	0	0	0.53	0.47
Columbina talpacoti	0	0	1	0
Crax fasciolata	0	0.98	0	0.02
Cyanocorax chrysops	0	0	0.53	0.47
Cyanocorax cyanomelas	0	0	1	0
Gnorimopsar chopi	0	0	1	0
Guira guira	0	0	1	0
Icterus croconotus	0	0	0.53	0.47
Myiarchus ferox	0	0	0.53	0.47
Myiodynastes maculatus	0	0	0.53	0.47
Ortalis canicollis	0	0	1	0
Paroaria coronata	0	0	0.53	0.47
Pipile jacutinga	0	0	1	0
Pitangus sulphuratus	0	0	0.53	0.47
Psarocolius decumanus	0	0	1	0
Pteroglossus castanotis	0	0	1	0
Ramphastos toco	0	0	1	0
Ramphocelus carbo	0	0	1	0
Rhea americana	0.15	0.79	0	0.06
Saltator coerulescens	0	0	0.53	0.47
Tachyphonus rufus	0	0	1	0
Thraupis palmarum	0	0	0.53	0.47
Thraupis sayaca	0.06	0	0.47	0.47
Trogon curucui	0	0	0.53	0.47
Turdus rufiventris	0	0	0.53	0.47
Turdus sp.	0	0	1	0
Tyrannus melancholicus	0	0	0.53	0.47
Tityra cayana	0	0	0.53	0.47
Alouatta caraya	0	0.97	0.01	0.02
Cerdocyon thous	0	1	0	0
Dasyprocta sp.	0.53	0.45	0	0.02
Mazama americana	0	0.98	0	0.02
Nasua nasua	0	0.98	0	0.02
Pecari tajacu	0	0.98	0	0.02
Procyon cancrivorus	0	1	0	0
Tapirus terrestris	0	1	0	0
Tayassu pecari	0	0.98	0	0.02
Geochelone carbonaria	0	0.98	0	0.02
Piaractus	0.87	0	0.05	0.08

mesopotamicus				
Artibeus sp.	0.01	0	0.92	0.07
*Eremotherium laurillardi**	0.98	0.02	0	0
*Stegomastodon waringi**	0.98	0.02	0	0
*Glossotherium lettsomi**	0.98	0.02	0	0
Xenorhinotherium sp.*	0.98	0.02	0	0
*Palaeolama major**	0.98	0.02	0	0

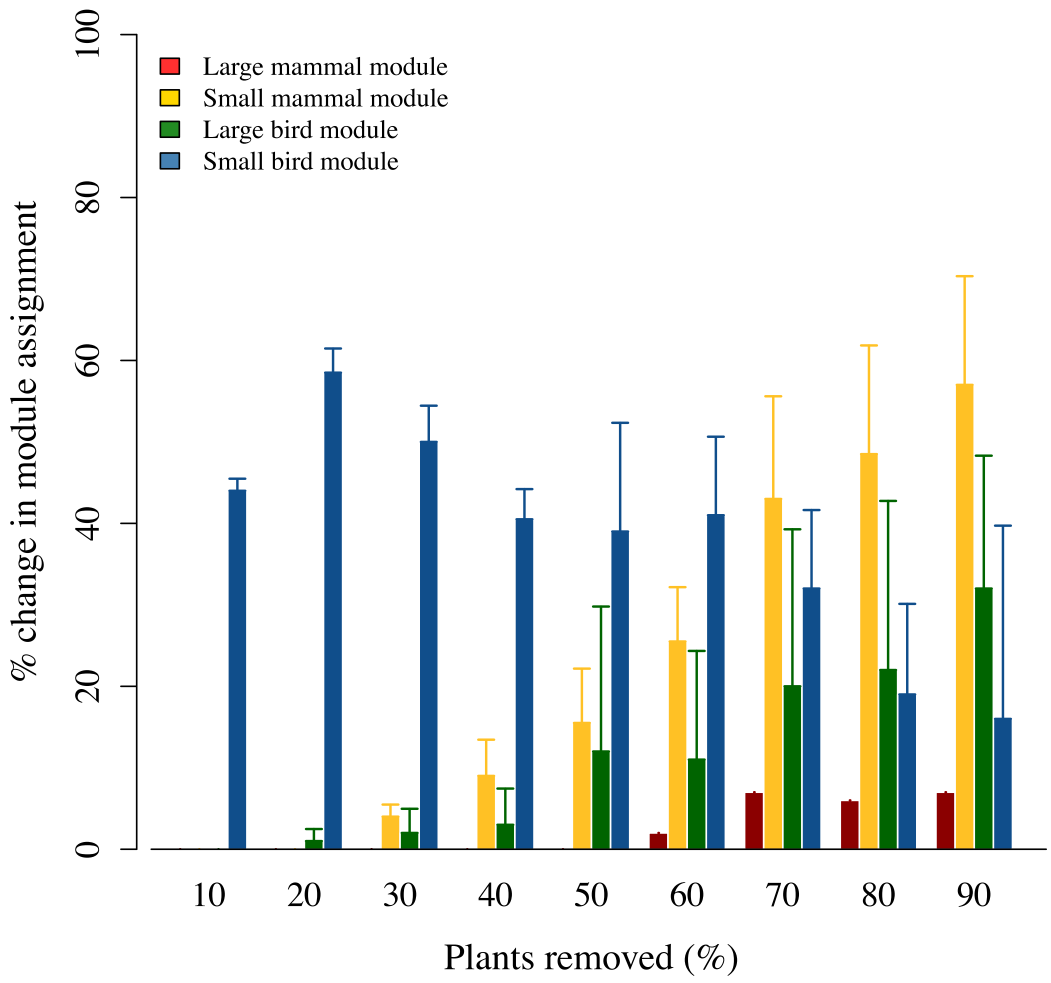

Figure S1. Robustness of modules to changes in vegetation. Frequency with which seed dispersers in a given module in the Pleistocene seed-dispersal network were assigned to a different module after plants were removed (Appendix S2). Filled bars denote the median considering all the species originally in a given module and error bars denote the median absolute deviation.

CONSIDERAÇÕES FINAIS

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As diferentes seções que compõem a tese abordam aspectos relacionados a organização de redes de interações ecológicas de diferentes tipos e, mais especificamente, aos mecanismos e consequências relacionados à extinção de mamíferos do Pleistoceno:

- Nossos resultados com modelos de teias tróficas sugerem que diferentes tipos de interações ecológicas, como interações mutualísticas entre plantas e dispersores de sementes e interações antagonísticas entre predadores e presas, são organizadas por processos similares. Além disso, mostramos a importância do grau de intimidade das interações na organização das redes ecológicas e como modelos de teias tróficas podem ser adaptados para reproduzir diversos tipos de sistemas incluindo sistemas do passado. As modificações dos modelos de teias tróficas, o desenvolvimento de abordagens para testar seu desempenho e a integração dos modelos com informações sobre a biologia dos sistemas de estudo criam as bases para futuros estudos sobre como aspectos básicos da biologia dos organismos organizam redes ecológicas.

- Os sistemas naturais que vemos hoje são uma consequência de processos ecológicos e evolutivos que os modificaram com o tempo. Para compreender os mecanismos responsáveis por extinções e mudanças na estrutura das comunidades ecológicas é necessário olhar não somente para os fatores externos às comunidades, mas também para suas propriedades intrínsecas. Nossos resultados sugerem que as interações nas comunidades de grandes mamíferos do Pleistoceno provavelmente estavam organizadas de forma similar às interações nas comunidades atuais na África. Entretanto, diferenças na composição e na distribuição de massas corpóreas fariam com que essas comunidades fossem especialmente sensíveis a certos tipos de perturbações, como a invasão de um grande predador como o homem. Nossas simulações mostram ainda como diferentes combinações de efeitos de mudanças climáticas e da chegada do homem poderiam, por meio de efeitos diretos e indiretos mediados por interações interespecíficas, resultar no colapso de comunidades do Pleistoceno. Esse conjunto de resultados dá embasamento quantitativo a hipóteses propostas previamente para explicar as extinções do Pleistoceno. Nós sugerimos que são necessários estudos como este, integrando abordagens quantitativas e conhecimento paleontológico e ecológico, para entendermos melhor como a interação entre fatores extrínsecos e intrínsecos influenciaram a dinâmica de sistemas do passado.

- As extinções do Pleistoceno tiveram uma série de consequências ecológicas, influenciando a composição de comunidades vegetais e processos como ciclagem de nutrientes e a dispersão de sementes. O estudo das mudanças em uma rede de dispersão de sementes após a extinção dos grandes mamíferos do Pleistoceno, permitiu avaliar como extinções podem impactar a estrutura de outros tipos de redes ecológicas, influenciando tanto plantas – potencialmente alterando padrões de recrutamento – quanto animais – por modificar seu papel na rede de interações. Abordagens como as utilizadas neste estudo, que permitiram reconstruir e avaliar as propriedades de comunidades do passado, são essenciais para entendermos as consequências de episódios de extinção, tanto no passado quanto atuais.

O presente estudo contribui para a compreensão dos processos que organizam interações ecológicas e enfatiza a importância das interações entre espécies para a dinâmica de comunidades ecológicas. De maneira geral, o conjunto de resultados apresentado e discutido aqui ressalta que para compreendermos as causas e consequências de extinções biológicas, tanto do passado quanto atuais, é necessário considerar as propriedades dos sistemas nos quais os organismos de interesse estão inseridos.