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PLANT-MICROBE-ANIMAL INTERACTIONS - ORIGINAL RESEARCH

Reconstructing past ecological networks: the reconfiguration of seed-dispersal interactions after megafaunal extinction

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Abstract The late Quaternary megafaunal extinction impacted ecological communities worldwide, and affected key ecological processes such as seed dispersal. The traits of several species of large-seeded plants are thought to have evolved in response to interactions with extinct megafauna, but how these extinctions affected the organization of interactions in seed-dispersal systems is poorly understood. Here, we combined ecological and paleontological data and network analyses to investigate how the structure of a species-rich seed-dispersal network could have changed from the Pleistocene to the present and examine the possible consequences of such changes. Our results indicate that the seed-dispersal network was organized into modules across the different time periods but has been reconfigured in different ways over time. The episode of megafaunal extinction and the arrival of humans changed how seed dispersers were distributed among network modules. However, the recent introduction of livestock into the seed-dispersal system partially restored the original network organization by strengthening the modular configuration. Moreover, after megafaunal extinctions, introduced species and some smaller native mammals became key components for the structure of the seed-dispersal network. We hypothesize that such changes in network structure affected both animal and plant assemblages, potentially contributing to the shaping of modern ecological communities. The ongoing extinction of key large vertebrates will lead to a variety of context-dependent rearranged ecological networks, most certainly affecting ecological and evolutionary processes.

Keywords Ecological networks · Frugivory · Modularity · Mutualisms · Pantanal · Rewilding

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Introduction

The species in a community form a network of interactions whose structure has implications for the ecological and evolutionary dynamics of the populations (May 1972; Pimm 2002; Dunne 2006; Bascompte and Jordano 2007). 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 can be highly robust to extinctions (Dunne et al. 2002; Memmott et al. 2004). Similarly, studies on the effects of species invasions and on the spatial and 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 (Olesen et al. 2008; Petanidou et al. 2008; Vilà et al. 2009). Nonetheless, when a considerable number of species is lost, because of changes in distribution or extinctions, major changes in network structure and consequently in network dynamics are expected.

The disruption of ecological networks is a possible outcome of large extinction events in which many species and their interactions are removed from the community within a relatively short time when compared to background extinctions. A representative example of a drastic change in community composition is the late Quaternary extinction (LQE) of the megafauna (body mass ≥44 kg) that occurred close to the Pleistocene-Holocene transition [between 50,000 and 10,000 years ago (Martin and Klein 1984)]. In South America alone, approximately 50 genera of large-bodied mammals went extinct (Koch and Barnosky 2006; Barnosky and Lindsey 2010). Although many studies have focused on the causes underlying the LQE (Koch and 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 and 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 and 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 and 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 ongoing defaunation will affect ecological processes (Galetti and Dirzo 2013).

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 and Shockey 1997; MacFadden 2000) and information on plant traits and 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 and Klein 1984), we expected that network organization in the Pleistocene would be substantially different and would have experienced 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 reconfigure an ecological network.

Materials and methods

Study site

The seed-dispersal interactions were surveyed in two neighboring locations in the Brazilian Pantanal: Rio Negro (19°34′S 56°14′W) and Barranco Alto farms (19°34′S 56°09′W), covering 7,500 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 and Soares 2004) that resulted in vegetation shifts (Whitney et al. 2011). Although such changes most certainly affected plant communities, palynological data show that by 19.5 thousand years before the present, when tropical forest communities began to expand following the full glacial period, 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 these 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 and Lindsey 2010). The estimated body masses were obtained from the literature (Smith et al. 2003; Online Resource 1). Dietary data were compiled from feeding ecology studies of each taxon (Online Resource 1). When estimated body mass or diet of a given species was not available, we used information on closely related taxa.

Archaeological 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 there is evidence of the use of fruits of several species by indigenous people over the long term (Scoles and Gribel 2011).

The network time series

We used the seed-dispersal network sampled by Donatti et al. (2011). This data set 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 (M. Galetti, unpublished 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: the plant-frugivore network in the late Pleistocene, after the expansion of tropical forest communities, following the full glacial (Whitney et al. 2011); the early Holocene network in which most megafaunal species died out and paleoindians already inhabited the region; the Colonial period (1800s), 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 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 interaction patterns of species that are now extant did not change across time periods, 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 of their diets (MacFadden and Shockey 1997; Online Resource 1). 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 these 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 and Martin 1982; Janzen 1984), by restricting megafaunal interactions to these 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

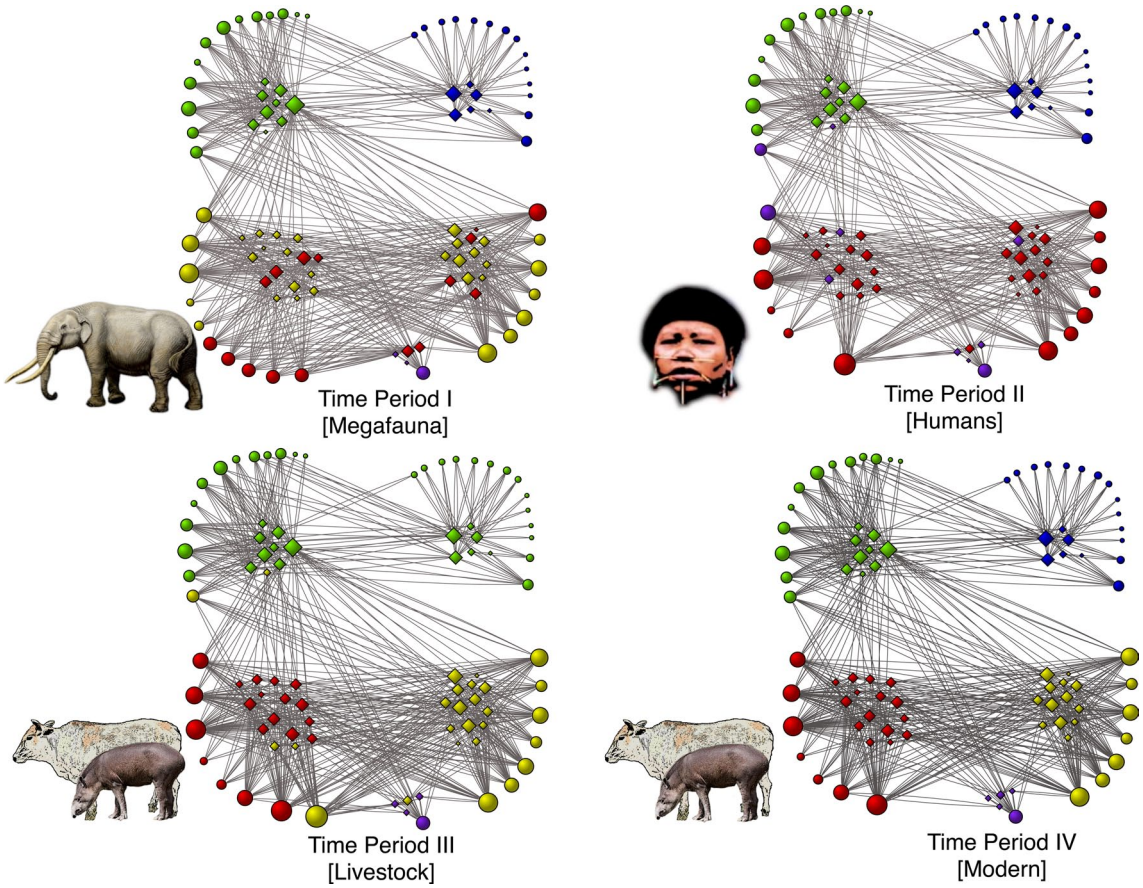

Fig. 1 Seed-dispersal networks representing different time periods in the network time series. *Nodes* represent animals (*circles*) and plants (*diamonds*) and the *size* of a node is proportional to its number of interactions. *Colors* identify the modules to which each species is assigned. *Green* 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 Online Resource 5 for the species composition of each module

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 NODF index (a nestedness metric basedon overlap and decreasing fill) (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 a simulated annealing algorithm to maximize the index of modularity (M) (Guimerà and Amaral 2005). M equals 0 if species are placed at random into modules and approaches 1 if there are few between-module interactions. There are different metrics available to compute modularity (Thébault 2013; Marquitti et al. 2014). We opted to use M because it has been widely used in the literature of mutualistic networks (including Donatti et al. 2011), and thus, using M allows comparisons across studies. M does not take into account the fact that seed-dispersal networks are two-mode networks, but it is also suited to estimate modularity of two-mode networks (Olesen et al. 2007). 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). Using a null model that accounts for the two-mode nature of mutualistic networks is essential when dealing with this type of network; otherwise the theoretical networks built under the null scenario are unrealistic and significance tests can lead to wrong conclusions (Fortuna

et al. 2010; Pires et al. 2011). In addition, we performed a second set of analysis, using a different metric specially designed for two-mode networks (Barber 2007). The results with this second metric do not alter our main findings (Online Resource 2).

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 modular organization of networks 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 and 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 extinct megafauna would interact with the same subset of available fruits, which results in the total overlap of interaction patterns. This overlap may impact the network structure in non-obvious ways. For instance, megafaunal species could form an additional module with the megafaunal fruits. Alternatively, if megafaunal fruits are in different modules in the modern network, adding several species with a similar interaction pattern could merge such modules, potentially reducing modularity. Nevertheless, it is unlikely that all megafaunal species fed on exactly the 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 on a variable set of non-megafaunal fruit species in addition to megafaunal fruits (Online Resource 3).

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 end of the Pleistocene and today (see "Study site"), we performed an additional analysis to test whether our results were robust when this assumption is relaxed (Online Resource 4). 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 was 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 (Online Resource 1) 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 (Online Resource 5).

All the networks in the time series were both more nested and more modular than expected by the null model (Fig. 2). However, the number and composition of the modules changed across networks (Online Resource 5). 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 ($1.6 \times 10^3 \pm 2.2 \times 10^3$ 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 ($M = 0.368 \pm 0.006$). Nevertheless, the module organization of the two mammal-dominated modules is consistent even when considering that megafauna

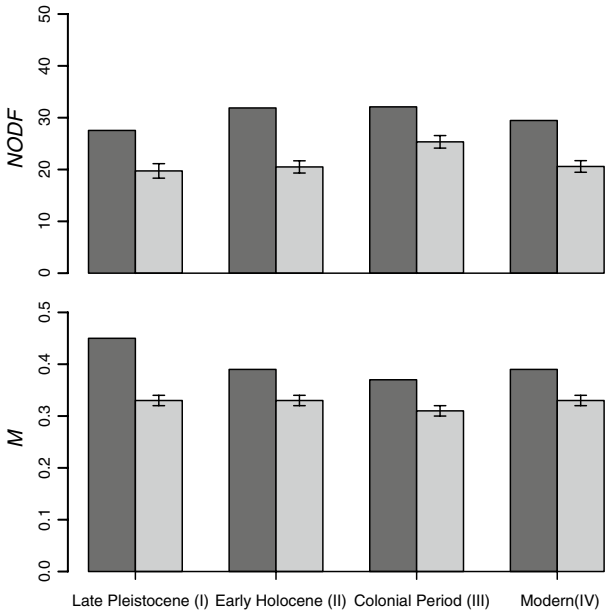

Fig. 2 Nestedness (*NODF*) and modularity (*M*) of the seed-dispersal networks representing each time period in the time series (*black bars*) and the average nestedness and modularity for networks built under the null scenario (*gray bars*). *Errors bars* depict the SD of the null distributions

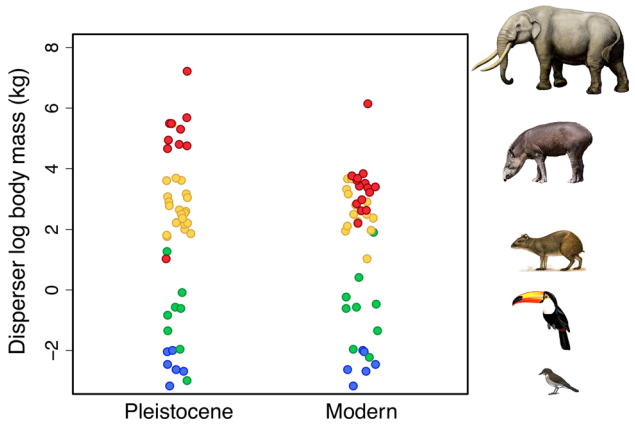

Fig. 3 Average body size of dispersers of each plant species in the Pleistocene and modern seed-dispersal networks. *Colors* indicate the module to which each plant species was assigned: *red* large mammal-dominated module, *yellow* small mammal-dominated module, *green* large bird-dominated module, and *blue* small bird-dominated model

would have interacted with several other plant species that do not fit the megafaunal dispersal syndrome (see table in Online Resource 3). 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 (see figure in Online Resource 4).

In the second major period, after the megafaunal extinction, paleoindians, by interacting with a considerable proportion of the plant species, would have increased the connectivity between the module previously dominated by megafauna and the other modules (Fig. 1). Conversely, the arrival of livestock (pigs and cattle) in the third period (Colonial period) would have restored the cohesion of the large mammal module by increasing the proportion of interactions within the module. Finally, in the modern time period, a time when humans are no longer relevant as dispersers, but cattle and feral pigs still act as seed dispersers, the network is, again, best characterized by five well-defined modules (Fig. 1).

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; Online Resource 5). 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. 3). 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. 3).

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. 3). This is also true for the topological 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. 4). 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 azarae*), 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. 4).

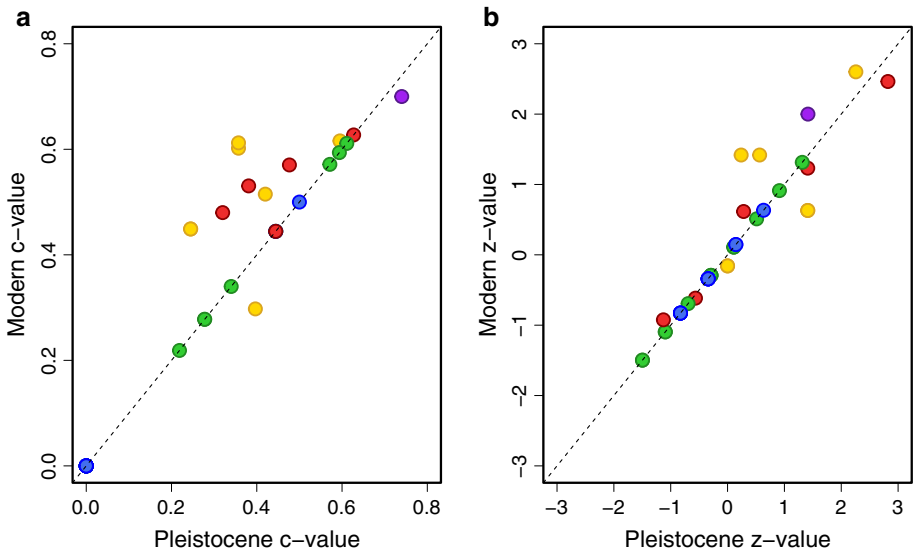

Fig. 4 Network roles of extant species in the modern and Pleistocene seed-dispersal networks. The metric *c* measures the inter-module connectivity (**a**), and *z* measures intra-module connectivity (**b**). *Colors* indicate the modules that each species is assigned to in the modern network (following the color scheme of Figs. 1 and 3). 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 Pleistocene megafauna that became extinct in the Neotropics were potential seed dispersers of extant plant species (Janzen and 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. 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, increasing the connectivity between species in the two modules dominated by mammals. The organization of the network would have been partially restored after the introduction of exotic species (pigs and cattle), which disperse the seeds of many of the plants presumably dispersed by Pleistocene megafauna (Janzen and Martin 1982; Donatti et al. 2011).

The introduction of surrogate seed dispersers has been suggested as a management tool to locally restore ecological and evolutionary processes in those areas where large vertebrates died out (Galetti 2004; Donlan et al. 2006; Griffiths et al. 2011). Although our results suggest that livestock and feral pigs could have partially restored the structural properties of the Pantanal seed-dispersal network, these meso-herbivores are considerably smaller than most of the extinct large herbivores (Zaya and Howe 2009). Among the extinct animals, the truly megaherbivores presumably impacted vegetation in different ways, such as imposing top-down effects that shaped the plant communities (Owen-Smith 1987; Asner et al. 2009). The extent to which exotic species are able to compensate for the loss of Pleistocene megafauna and their multiple ecological services remains to be tested.

In a modular system, species are tightly connected to other species in the same module, but loosely connected to the rest of the network (Olesen et al. 2007). As a result, the effects of structural changes in modular systems should be stronger within the module where changes occurred instead of spreading to the whole network (Krause et al. 2003). Changes in the modular arrangement have thus the potential to affect how the effects of perturbations, such as changes in the density of populations or extinctions, spread across the system. Network organization, and modularity in particular, also has implications for evolutionary dynamics. Theory predicts species connected directly and indirectly may affect the rates of phenotypic evolution of each other through coevolutionary cascades (Guimarães et al. 2011). Species in different modules are connected via a smaller number of pathways and thus are less likely to affect each other in terms of the rates of evolutionary processes (Guimarães et al. 2011). In this sense, the evolutionary consequences of megafaunal extinction would have been different for species in different modules. Megafaunal extinctions increased the reliance of large-seeded plants on smaller seed dispersers, potentially shifting selection regimes by benefiting phenotypes with smaller seeds. This phenomenon has been reported in modern seed-dispersal systems that lost large frugivorous birds and may have implications for seed germination and recruitment (Galetti et al. 2013). Whether or not a similar phenomenon happened in response to megafaunal extinctions is a question that warrants further research.

Pleistocene and modern networks would be very dissimilar in at least one additional 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 (Vidal et al. 2013). Large frugivores are the main seed dispersers of seeds that are too large for smaller mammals and birds (Janzen and Martin 1982; Hansen and Galetti 2009) and are more likely to promote long-distance dispersal, connecting plant populations across fragmented landscapes (Nathan and 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 for. Here, we did not attempt to estimate the quantitative contribution of extinct megafauna to seed dispersal and focused on the topology of qualitative networks that describe who interacts with whom. It is important to note that even species in the same modules, i.e., similar interaction patterns, may have different effects in terms of the frequency and effectiveness of interactions (e.g., Brodie et al. 2009; Bueno et al. 2013). Future studies incorporating such aspects will go a step further in indicating the effects of structural changes in the seed-dispersal network on seed-dispersal systems.

Although we focus here on seed-dispersal interactions between the plants and seed dispersers, species are connected via different types of interactions. In this sense, the megafaunal extinction may have had far-reaching impacts for plants and seed dispersers that are in different modules of the seed-dispersal network. We hypothesize that, as the recruitment of plants that relied on megafaunal species decreased due to seed-dispersal limitation, those plants that are dispersed by other primary and secondary dispersers (e.g., birds and rodents), possibly faced lower competition and higher probabilities of recruitment. These consequences would thus be positive indirect effects of the megafaunal extinction for 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 the late Pleistocene (Whitney et al. 2011). Although this vegetation shift is likely related to changes in climate conditions, the loss of megafauna could have contributed in different ways (e.g., Doughty et al. 2013; Gill 2013). Large herbivores, such as elephants and rhinoceros have an important role in maintaining the open savanna environments in Africa (Owen-Smith 1987). Similarly, the expansion of sclerophyllous vegetation in Australia has been associated with the demise of the Australian megafauna (Rule et al. 2012). These and other similar effects are often associated with the top-down control imposed by megafauna herbivores (Terborgh and Estes 2010). The effects of the loss of megafauna on seed dispersal discussed here represent another route by which megafauna extinction could have shaped modern plant communities.

A related 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). Recent studies suggest a similar pattern in the African lowland forests (Effiom et al. 2013). As better data on the composition of the plant communities in the past are obtained from the fossil record, future studies should be able to test whether a shift in plant composition followed the Pleistocene megafaunal extinction in South America, 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 over time. The megafauna-dispersed 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 rhinoceros 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 a 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 and might disrupt the multiple roles (beyond seed dispersal) of large mammals in shaping plant communities.

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