

PERSPECTIVES

Beyond species loss: the extinction of ecological interactions in a changing world

Alfonso Valiente-Banuet^{*1}, Marcelo A. Aizen², Julio M. Alcántara³, Juan Arroyo⁴, Andrea Cocucci⁵, Mauro Galetti⁶, María B. García⁷, Daniel García⁸, José M. Gómez^{9,10}, Pedro Jordano¹¹, Rodrigo Medel¹², Luis Navarro¹³, José R. Obeso⁸, Ramona Oviedo¹⁴, Nelson Ramírez¹⁵, Pedro J. Rey³, Anna Traveset¹⁶, Miguel Verdú¹⁷ and Regino Zamora¹⁰

¹Departamento de Ecología de la Biodiversidad, Instituto de Ecología, Universidad Nacional Autónoma de México, Ap. Postal 70-275, México, 04510 DF, México; ²Laboratorio Ecotono-CRUB, Universidad Nacional del Comahue and INIBIOMA, 8400, San Carlos de Bariloche, Río Negro, Argentina; ³Departamento de Biología Animal, Biología Vegetal y Ecología, Universidad de Jaén, E-23071 Jaén, Spain; ⁴Departamento de Biología Vegetal y Ecología, Universidad de Sevilla, Apdo. 1095, E-41080 Sevilla, Spain; ⁵Laboratorio de Biología Floral, Instituto Multidisciplinario de Biología Vegetal (IMBIV), CONICET-Universidad Nacional de Córdoba, Casilla de Correo 495, 5000 Córdoba, Argentina; ⁶Departamento de Ecología, Universidade Estadual Paulista (UNESP), 13506-900 Rio Claro, Sao Paulo, Brazil; ⁷Instituto Pirenaico de Ecología, CSIC, Apdo. 13034, E-50080 Zaragoza, Spain; ⁸Departamento de Biología de Organismos y Sistemas, Universidad de Oviedo, Unidad Mixta de Investigación en Biodiversidad (UMIB CSIC-UO-PA), E-33071 Oviedo, Spain; ⁹Departamento de Ecología Funcional y Evolutiva, Estación Experimental de Zonas Áridas (EEZA-CSIC) Ctra Sacramento s/n, La Cañada de San Urbano, E-04120 Almería, Spain; ¹⁰Departamento de Ecología, Facultad de Ciencias, Universidad de Granada, E-18071 Granada, Spain; ¹¹Integrative Ecology Group, Estación Biológica de Doñana (EBD-CSIC), Avda. Americo Vespucio s/n, Isla de La Cartuja, E-41092 Sevilla, Spain; ¹²Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Casilla 653, Santiago, Chile; ¹³Department of Plant Biology and Soil Sciences, Faculty of Biology, University of Vigo, As Lagoas-Marcosende, E-36200 Vigo, Spain; ¹⁴Instituto de Ecología y Sistemática de La Habana, Carretera Varona 11835 e/ Oriente y Lindero, La Habana 19, Cp. 11900, Calabazar, Boyeros, Cuba; ¹⁵Facultad de Ciencias, Instituto de Biología Experimental, Universidad Central de Venezuela, Aptdo. 48312, Caracas 1041A, Venezuela; ¹⁶Terrestrial Ecology Group, Laboratorio Internacional de Cambio Global (LINC-Global), Institut Mediterrani d'Estudis Avançats (CSIC-UIB), C/Miquel Marqués 21, E-07190, Esporles, Mallorca, Balearic Islands, Spain; and ¹⁷Centro de Investigaciones sobre Desertificación (CIDE CSIC-UV-GV), Apartado Oficial, E-46113 Moncada, Valencia, Spain

Summary

1. The effects of the present biodiversity crisis have been largely focused on the loss of species. However, a missed component of biodiversity loss that often accompanies or even precedes species disappearance is the extinction of ecological interactions.
2. Here, we propose a novel model that (i) relates the diversity of both species and interactions along a gradient of environmental deterioration and (ii) explores how the rate of loss of ecological functions, and consequently of ecosystem services, can be accelerated or restrained depending on how the rate of species loss covaries with the rate of interactions loss.
3. We find that the loss of species and interactions are decoupled, such that ecological interactions are often lost at a higher rate. This implies that the loss of ecological interactions may occur well before species disappearance, affecting species functionality and ecosystems services at a faster rate than species extinctions. We provide a number of empirical case studies illustrating these points.
4. Our approach emphasizes the importance of focusing on species interactions as the major biodiversity component from which the ‘health’ of ecosystems depends.

Key-words: biotic interactions, co-evolution, diversity, extinction debt of ecological interactions, global change drivers

*Correspondence author. E-mail: avalient@ecologia.unam.mx

Introduction

Understanding the factors behind biodiversity loss is one of the most urgent tasks faced by scientists at present. Fast-paced rates of habitat loss and fragmentation, and large-scale disturbances (e.g. biological invasions, habitat degradation, recurrent defaunation) are presently the main anthropogenic drivers of species extinctions. Current estimates of species extinctions are three to four orders of magnitude above background extinction rates (Barnosky *et al.* 2011). Recent estimates of extinction risk from a wide range of climate impacts and ecosystem types indicate that real empirical data often exceed predicted extinctions (Maclean & Wilson 2011), which suggests that we are still far from having adequate tools to predict species losses attributable to major anthropogenic disturbances such as habitat loss (He & Hubbell 2011). Furthermore, many species now survive at such low densities that they can be considered practically extinct from an ecological point of view (Janzen 2001). These limitations preclude an adequate assessment of ecosystem functions decays, and their derived services, an emerging research field where species richness is the diversity metric (Balvanera *et al.* 2006; Cardinale *et al.* 2012).

Biodiversity loss has been largely assessed through species extinctions. However, an important yet frequently missed component of biodiversity loss that goes along or may even precede species extinctions is the extinction of ecological interactions in which those species are engaged (Janzen 1974; Tylianakis *et al.* 2008; Aizen, Sabatino & Tylianakis 2012). Given that many key functional aspects of ecosystems closely depend on biotic interactions, their loss may have pervasive effects accelerating species local extinction and decay of ecosystem functions, ultimately collapsing the derived services provided to humans (Díaz *et al.* 2013). Moreover, extinctions of interactions and their associated ecological functions may frequently precede the complete disappearance of species, that is, when a species' abundance is so reduced as to represent its functional extinction (Redford 1992; Janzen 2001; Wilkie *et al.* 2011; Galetti *et al.* 2013; Säterberg, Stellan & Ebenman 2013). Biotic interactions are thus a major but often neglected component of biodiversity that needs to be considered in order to assess the 'health' of ecosystems and to define critical indicators providing early diagnosis of environmental problems (Tylianakis *et al.* 2010; Aizen, Sabatino & Tylianakis 2012; Dirzo *et al.* 2014). Several studies have already demonstrated that species interactions are particularly sensitive to different anthropogenic drivers often shifting their frequency or becoming disrupted due to large environmental changes (Tylianakis *et al.* 2008). In consequence, there is an urgent need to develop robust analytical tools, such as generic mechanistic models, to understand, foresee and manage the impact of anthropogenic drivers on biotic interactions.

Under this conceptual framework, and based on a set of proposed definitions, here, we model the relationship between both the diversity of species and interactions along a gradient of habitat loss (as a generic form of environmental degradation) and examine the consequences of interaction extinctions for the maintenance of ecological functions. We assume that species extinctions increase with increasing habitat loss, the signature conservation problem of the twenty-first century (He & Hubbell 2011). Other scenarios where species gains occur after habitat loss (e.g. invaded sites having higher levels of diversity than pristine sites; Lekberg *et al.* 2013; Stouffer, Cirtwill & Bascompte 2014) are not considered here, but extensions of the proposed model could account for these situations. In our model, we apply the concept of extinction debt of species to ecological interactions [see original definitions in Tilman *et al.* (1994) and Wearn, Reuman & Ewers (2012)]. Accordingly, we define the *extinction debt of ecological interactions* as any future interaction loss that has to be realized due to a current or past environmental disturbance. Our concept refers to those interactions 'committed to extinction' owing to lags between the habitat loss and the complete extinction of the interaction. We refer to extinction of an interaction when its ecological outcomes are no longer functional, for example collapse of fruit set and/or fruit removal, loss of long-distance dispersal. For example, extensive declines of megafauna frugivores due to habitat fragmentation might represent future functional losses of seed dispersal services (Bueno *et al.* 2013), even when the species themselves and their interactions remain sporadically recorded in biodiversity inventories. Here, we show that interaction-based extinction debts emerge as a consequence of the different pace for species and interactions extinctions. The mismatch between species and interaction extinction curves determines the response of ecological functions, depending on how crucial is their functional effect in local communities.

Shifting the focus from species to ecological interactions

The extinction of species inevitably causes the loss of interactions in which they are involved. In this situation, the number of interactions disappearing due to habitat loss can be assumed to be proportional to the number of species going extinct, a situation we call *directly proportional interaction loss*. However, this assumption may not be necessarily well warranted as it implies that (i) species are equivalent in terms of the number and quality of their interactions, (ii) species cannot survive, at least temporarily, despite becoming mostly disconnected from others and (iii) the emergence of new interactions does not occur. In this oversimplified scenario, which can serve as a null hypothesis, the set of interactions is viewed as static and homogeneously structured. To explore the broad array of situations where the number of interactions lost does not follow linearly the number of species disappearing from

the community, we have developed a model that takes into account the way interactions are lost as a function of habitat loss (Box 1). Our model allows examining the consequences of an increased or decreased loss of interactions relative to the number expected under directly proportional interaction loss, that is *interaction balance* (Fig. 1c). The interaction balance, in turn, depends on a single parameter, which we call delta (ΔL), a property of the community that reflects its resistance or susceptibility to interaction losses regarding species loss. In other words, delta indicates how much faster or slower the speed of interaction loss is with respect to a proportional loss. When delta is negative, interactions are lost at a lower rate than species along the gradient of habitat loss, and thus, the interaction balance is positive (Fig. 1c). We call this situation *interaction surplus*. In contrast, when delta is positive, interactions are lost at a higher rate than species along the gradient of habitat loss, and the resulting interaction balance is negative (Fig. 1c). We call this situation *interaction deficit*.

Interaction surplus occurs when the average number of interactions per species (degree) of a community that has been subjected to habitat loss is greater than before habitat loss. This phenomenon may result from two non-mutually exclusive mechanisms. First, if the surviving species build up new interactions (i.e. 'rewiring' in network terminology), then the directly proportional interaction loss may be overcompensated, increasing the linkage density (Pimm, Lawton & Cohen 1991). For example, many plants are visited by few and efficient pollinators that competitively

exclude less effective pollinators (Mitchell *et al.* 2009). In these systems, the loss of a main pollinator entails that less efficient and otherwise competitively excluded animals broaden their list of floral resources by pollinating new plant species or populations (Pérez-Barrales, Vargas & Arroyo 2006; Pérez-Barrales & Arroyo 2010). Likewise, if a magnet plant species is removed from a community, pollinators may compensate its suppression by building up new interactions with other plant species to which they were not attracted before (Kaiser-Bunbury *et al.* 2010). Secondly, when species extinction is biased towards the less connected species and the connections among the surviving species remain unaltered after disturbance, we might expect a surplus of interactions relative to the situation before disturbance. For instance, pollination and seed dispersal webs can remain with surplus connectivity in isolated and fragmented areas, as species number decreases and generalists survive better than specialists (Hagen *et al.* 2012). Similarly, the mean number of plant-plant facilitation interactions may increase in a community after the local extinction of the less connected nurse plants because facilitated species are able to recruit under generalist nurse species (Verdú & Valiente-Banuet 2008; Valiente-Banuet & Verdú 2013). Finally, interaction surplus may occur when the loss of interactions caused by the extinction of a key species promotes the emergence of new interactions of a different type. In many communities, competition between plant species is cancelled by the presence of a generalist keystone herbivore that keeps plant abundance below a critical threshold. Removal of the keystone herbivore may

Box 1: Predicting interaction losses in a changing world

We define an axis of habitat loss (x) that ranges from a pristine, undisturbed stage (zero) to a stage (one) of complete disturbance where all species present in the zero stage have lost their habitat. This axis may represent a reversed area axis, widely used to indirectly predict extinction rates with species-area curves (He & Hubbell 2011). It may also represent any axis of habitat deterioration, such as increased isolation of habitat fragments, degree of desertification and intensity of grazing. Along this axis, we represent the pattern of species loss as a function of species richness decrease (He & Hubbell 2011), $S(x)$, with α as the slope of this loss (Fig. 1a). To study how the pattern of species extinctions may affect the interaction extinctions, we translated species richness into an interaction or link loss function, $L(x)$, through the expression derived by (May 1972) and empirically corroborated in recent studies (Ings *et al.* 2009). It then follows that $L(x) = aS(x)^b$. Where 'a' is a proportionality factor which represents the per species number of links in the undisturbed stage, that is when habitat loss equals zero. According to the value of 'b', link loss from one stage to the next is faster or slower than species loss. Only when $b = 1$ is interaction loss proportional to species loss, thus, the amount of interaction loss proportionally contributed by species loss (directly proportional loss) may be dissected out from total interaction loss, that is for an $L(x)$ function with $b = 1 + \delta$ (Fig. 1b). Accordingly, we derive interaction balance ($\Delta L(x)$), that is the number of interactions in a community with a given degree of habitat loss in excess or deficit with respect to the expected number of interactions under exclusively directly proportional interaction loss. Interaction balance is given from the above expressions by $\Delta L(x) = a[S(x)^{1+\delta} - S(x)]$ which is represented as a unimodal curve (Fig. 1c). Interaction balance may represent an interaction surplus ($\Delta L(x) > 0$) when the community is resilient to interaction losses, whereas it may represent an interaction deficit ($\Delta L(x) < 0$) when the community is prone to cascading interaction losses. The stage of habitat loss where deficit or surplus is greatest shows critical points in the process of habitat degradation. Species loss or retention that is due to the effect of interaction balance we call species balance and is calculated as $\Delta S = \Delta L(x)/k(x)$, where $k(x)$ is the grade (mean number of interactions per species) at a given stage of habitat loss. This quantity tells about the number of species lost or retained as a consequence of accelerated or decelerated link loss.

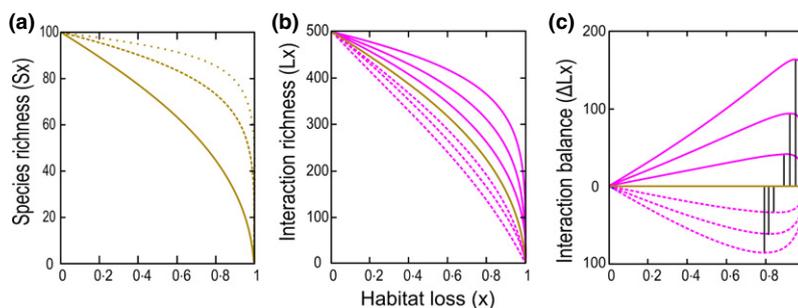


Fig. 1. (a) Species richness functions along an axis of increasing habitat loss (x) for three slope values, $\alpha = 0.1$ (dotted), $\alpha = 0.2$ (dashed) and $\alpha = 0.5$ (solid). (b) Interaction richness functions corresponding to a species richness function with $\alpha = 0.5$, number of species (S_0) and mean number of links (k_0) at $x = 0$ equal 100 and 5, respectively. For each, functions with values of b decreasing and increasing by $\delta > 0$ and $\delta < 0$ are represented above (dashed) and below (dotted) the directly proportional function ($b = 1$, solid line), respectively. (c) Interaction balance functions, $\Delta L(x)$, corresponding to the interaction richness functions in b. Vertical lines show the critical values of x where interaction deficit (below) or superavit (above) are greatest.

cause pairwise competitive interactions among all or most plant species to become manifest (Olf & Ritchie 1998). In this new situation, the number of competitive interactions in the herbivore-less community increases with respect to the original community.

In a second, non-mutually exclusive mechanism, interaction deficit may occur when habitat loss causes a reduction in the abundance of species down to a threshold below which the interactions are no longer maintained. For instance, many plants can escape predation and herbivory from generalist animals by living at very low densities (Greenwood 1985; Rooney 1997; Underwood & Halpern 2012). In such circumstances, the low densities of partners, making the actual encounter unlikely, may cancel potential antagonistic interactions. Likewise, interaction deficits may also occur in systems where many weak interactions are maintained by a core of strong mutualists (super-generalists) that enhance their abundance up to a threshold above which the weak interactions spontaneously arise (e.g. pollination and seed dispersal market). In this scenario, with many weak indirect interactions, the loss of one of such interactions will surely have only minor overall consequences. In contrast, the weakening of strong positive interactions between core species may trigger a decrease in the species' abundances, causing the loss of co-occurring weak interactions (Aizen, Sabatino & Tylianakis 2012). These interaction deficits are likely attributable to subtle variation in the abundance of generalized plant–animal mutualisms, such as some pollination and dispersal interactions, as they imply consumer–resource use interactions with marked frequency dependency (Holland & DeAngelis 2010).

Other systems where multiple interactions arise by the effect of a single species are likely to produce interaction deficits. For example, in communities shaped by facilitation, a benefactor (e.g. nurse plant species) facilitates the establishment of other species, causing spatially aggregated clumps of species where multiple interactions are established (Castillo, Verdú & Valiente-Banuet 2010). Human overexploitation, by reducing the abundance of a number

of key nurses, has triggered the loss of a disproportionately high number of interactions between nurses and facilitated species (Valiente-Banuet & Verdú 2013). Another source of interaction deficit occurs through phenological mismatches between interacting species when environmental changes disrupt the synchronization in the activity periods of interaction partners (Arroyo & Dafni 1995; Visser & Holleman 2001). The speed of this detrimental effect may be strongly variable relying on the indirect dependence of species to interactions. For instance, an increased fruit set in small remnant forests has been detected when spare populations of native bee pollinators are displaced by a high abundance of introduced honeybees, reducing the number of mutualistic interactions (González-Varo, Arroyo & Aparicio 2009). Increased geitonogamy by honeybees, however, conveyed higher selfing rates and reduced progeny performance in such forests (González-Varo *et al.* 2010). In some cases, anthropogenic disturbances leading to habitat fragmentation affecting pollinator and seed disperser communities have been shown to promote evolutionary change in populations rather than extinction (Murúa *et al.* 2010; Brys & Jacquemyn 2012; Galetti *et al.* 2013), although the generality and trajectory of the change is still poorly understood (Jacquemyn *et al.* 2012). In general, interaction deficits can be envisioned under many different scenarios of anthropogenic habitat loss where interaction loss precedes species extinction (Sabatino, Maceira & Aizen 2010). This is probably a very frequent situation, where interactions – more labile in their origination and maintenance – are more prone to failure than species under the continuous deterioration of the environment (Quental & Marshall 2013).

From interaction extinctions to functional loss

Interspecific interactions provide the raw material for relevant ecological functions that determine the dynamics of populations, communities and ecosystems. For instance, pollination, seed dispersal and plant–plant facilitation and competition may drive the trajectory and speed of ecological succession (Connell & Slatyer 1977; Verdú *et al.* 2009)

and the co-evolutionary dynamics of multispecies assemblages (Guimarães, Jordano & Thompson 2011). Moreover, the functional outcomes of biotic interactions, mainly pollination, seed dispersal or host–parasitoid relationships, have been recently signalled as relevant ecosystem services (Kremen *et al.* 2007). The effects of interaction loss on the delivery of ecological functions will depend on the relative contribution of each interaction type to the global function provided by the whole interaction assemblage. From this perspective, we identify here three types of interaction functionalities:

1. Additive interactions: An interaction is called additive when its loss impacts at least one species involved in the interaction, but has no indirect effects on the remaining links of the interaction network. This category is based on the functional singularity of interactions within communities. In other words, every interaction adds its singular contribution to the ecological function and contributes equally to the function maintenance. This is the case of extremely specialized interactions. The fig–fig wasp interaction is a good example of additive interactions (Weiblen 2002), as the pollination service of the fig-dominated community depends on the addition of singular contributions of every species-specific fig–fig wasp interaction. When interactions are additive, the functional loss is expected to be gradual, decreasing linearly relative to the interaction loss (See Box 2, Fig. 2a). Thus, we expect that an increasing intensity of the anthropogenic driver will trigger a proportional response of interaction loss and functional loss (Fig. 2b).

Box 2: Interaction loss and functional decay

Once we have derived the functions of link loss along an axis of habitat loss (Box 1), we may translate link loss into functional loss given the theoretical relationships between functionality and link richness. These relationships can be described by means of a power law function of accumulative functionality with increasing link richness, λ . This function is given by $F(\lambda) \propto \lambda^\gamma$ where γ modulates the interaction functionality in the network such that when $\gamma = 1$, $\gamma > 1$ or $0 < \gamma < 1$ the functional role is additive, keystone or redundant, respectively (Fig. 2a). By replacing in this function λ with $L(x)$ from Box 1, we obtain a relationship of functional loss along an axis of habitat loss as $F(x) \propto L(x)^\gamma$ or $F(x) \propto S(x)^{\gamma\lambda}$. In other words, the speed of functional loss along the axis of habitat loss equals that of link loss only when the role is additive ($\gamma = 1$), whereas functional loss may be exacerbated if its role is keystone ($\gamma > 1$) or delayed if it is redundant ($\gamma < 1$; Fig. 2b). In analogy to interactions balance, we may also define functional balance to denote situations when functionality is maintained above or below values expected by link loss, buffering or exacerbating functional collapses or functional debts.

2. Keystone interactions: An interaction is called keystone when it controls community or ecosystem function to a disproportionately higher extent than predicted from the abundance of interacting organisms (Helfield & Naiman 2006). This interaction type is expected in communities showing strong differences in the contribution of interspecific interactions to ecological function. Such is the case when generalized mutualists (often called super-generalists) are removed from plant–pollinator or plant–disperser networks. For example, scatter-hoarding rodents play a pivotal role in the dispersal of large-seeded species in neotropical rain forests, especially in those once dispersed by the extinct Pleistocene megafauna (Guimarães, Galetti & Jordano 2008; Jansen *et al.* 2012). In Amazonian forests, the overharvesting of the Brazilian nut (*Bertholetia excelsa*) may have important consequences not only for the recruitment of *B. excelsa* and agouti populations, but also for the entire scatter-hoarding dispersal service of other large-seeded tree species (Peres *et al.* 2003; Galetti *et al.* 2006). Similar examples have been reported for flying foxes, gorillas and elephants for which overhunting and habitat loss has resulted in a recruitment reduction of a significant number of large-seeded species (McConkey & Drake 2006; Beaune *et al.* 2013; Haurez, Petre & Doucet 2013). Moreover, predator–prey interactions can have effects at different levels affecting preys directly and plants indirectly in many different ways (Novaro, Funes & Walker 2000; Ripple & Beschta 2006; Anderson *et al.* 2011). Strong reduction of grazing by a few large domestic herbivores in the alpine habitats of European mountains during the last decades is causing the encroachment of man-made meadows and the shift upwards of the tree line (Améztegui, Brotons & Coll 2010), which inevitably implies the loss of a countless number of interactions associated to the very rich alpine meadows. The loss of a keystone interaction has a disproportionate impact on the associated ecological function (Fig. 2a). Thus, when a keystone interaction is disrupted along an increasing gradient of anthropogenic impact, the involved ecological function will decline at a faster rate than the loss of interactions (Fig. 2b).

3. Redundant interactions: Ecological interactions are redundant when their contributions to the community functioning are equivalent and replaceable, as most interactions are able to sustain the optimal function by themselves (Lawton & Brown 1993). Thus, all pollinators are interchangeable as they have the same effect on fruit set (Gómez & Zamora 1999; Fründ *et al.* 2013). This seems to be the case of several Sonoran desert cacti, such as cardon (*Stenocereus thurberi*) and saguaro (*Carnegiea gigantea*), in which pollination either by bats (cardon) or by birds and honeybees (saguaro) alone accounts for most reproductive success (Fleming *et al.* 2001). Similarly, this occurs for the pollination of the endemic alpine *Borderea pyrenaica*, which is successfully

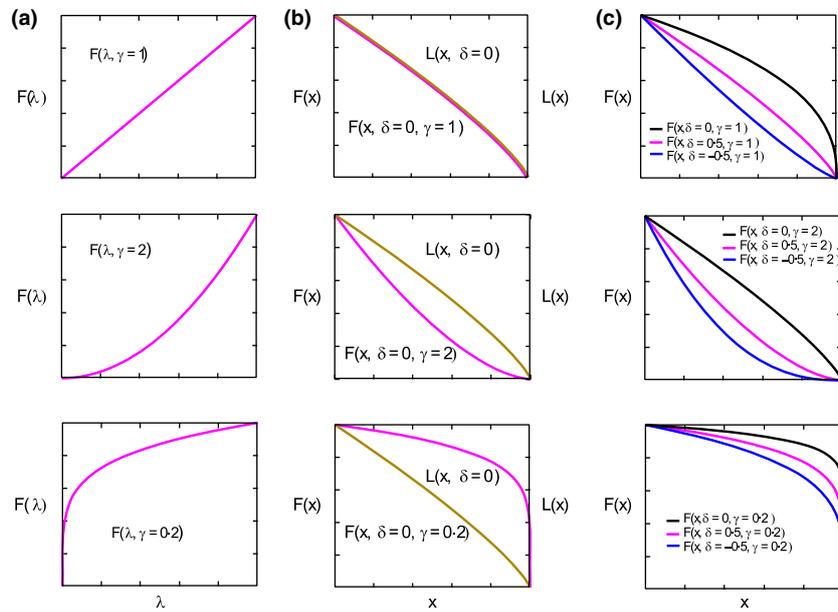


Figure 2. (a) Ecological function $F(\lambda)$ for interaction networks of variable size (λ), depending on three functional interaction roles (from top: additive, redundant and keystone). (b) Decay of ecological function (in magenta) along an axis of increasing habitat degradation, (x) depending on the additive, redundant and keystone role of interactions. The response of link richness to habitat loss $L(x)$ in a scenario of null interaction balance is shown, highlighting a functional collapse (for keystone role, the functional loss is faster than expected from interaction loss) or functional debt (for redundant role, the functional loss is slower than expected from interaction loss). (c) Functional decay for additive, redundant and keystone roles of interactions under different interaction balances (null in magenta, negative in black, positive in blue).

pollinated by the scarce resident ants, the years when the most abundant lady beetles do not arrive on time (García, Antor & Espadaler 1995). When an interaction is redundant, its loss will not reverberate in the ecological function of the interaction network, as long as other interactions substitute the role left by the lost one. Thus, ecological functions will be largely unaffected when the intensity of the anthropogenic driver is increased (Fig. 2b). Only when most interactions are lost, at high levels of the anthropogenic impact, will the ecological function finally collapse (Fig. 2b). The lag between environmental change and functional decay represents, therefore, an extinction debt for ecological functions (Fig. 2b).

Once we have established that the response of ecological function to anthropogenic change depends on the functional role of interactions, we may predict the functional loss expected under different scenarios of balance between interactions loss and species loss, that is, under situations of interaction surplus, deficit or null balance (Fig. 2c). Accordingly, positive and negative interaction balances will, respectively, exacerbate functional debts and functional collapses along the gradients of anthropogenic change.

The expected response of ecological functions along the habitat loss gradient would thus depend on the type of interaction scenario: surpluses in keystone scenarios vs. interaction deficits in redundant scenarios. This alone may buffer both functional losses and functional debts along the gradient, due to the multiplicative effect of interaction functionality and interaction balance.

For example, the redundancy among frugivores of *Prunus avium* in central Germany seems to maintain seed dispersal function across human-impacted landscapes despite changes in frugivore richness (Breitbach *et al.* 2012). On the other hand, an even stronger functional collapse is expected when the loss of keystone interactions is associated to concomitant interaction losses (i.e. interaction deficit). For example, the loss of the interaction of the palm *Maximiliana maripa* and its main seed disperser, the tapir *Tapirus terrestris*, in the Brazilian Amazonia leads to an additional loss of functionality in the secondary seed dispersal accounted by rodents feeding on seeds from tapir latrines (Fragoso 1997). On the other hand, a surplus of redundant interactions may lead to a longer functional debt. This seems to be the case in the interaction network between fleshy-fruited trees and frugivorous thrushes (*Turdus* spp.) in northern Spain. There, the decay of frugivory on the dominant tree *Ilex aquifolium* in low-crop years is compensated with stronger frugivory on the tree *Crataegus monogyna*, whose widespread distribution leads to an increased resilience of seed dispersal to habitat loss (García *et al.* 2013). A fast-paced loss of interactions ahead of species extinctions (i.e. an empty-forest syndrome; Janzen 1974; Redford 1992) will be clearly pervasive whenever extinction hits the keystone interactions.

Concluding remarks

In a changing world, habitat loss, climate change, severe defaunation and invasion of exotic species are the main

drivers of the present biodiversity crisis; the effects of which have been largely assessed by quantifying the loss of species. Despite considerable efforts of conservationists to secure viable populations of threatened species, their ecological extinction may have already occurred (Janzen 1974; Traveset & Riera 2005; McConkey & Drake 2006; Aslan *et al.* 2013; Galetti *et al.* 2013; Säterberg, Stellman & Ebenman 2013). Here, we applied a mechanistic model to demonstrate that the extinction of interactions can be decoupled from the extinction of species, fine-tuning the concept of co-extinction cascades of interacting species as a major form of biodiversity loss (Koh *et al.* 2004; Rezende *et al.* 2007; Dunn *et al.* 2009). More specifically, we suggest that such decoupling can be negative or positive, which means that interactions can be lost faster or go along the loss of species. In consequence, the rate of species extinction may be delayed or accelerated depending on the balance of interaction losses.

Our model shows that a critical aspect of how the loss of interactions impacts biodiversity depends on the balance between the rate at which interactions are lost relative to the loss of species. Losing interactions mean losing ecological functions, and the magnitude of the extinction debt due to the extinction of interactions can exceed the proportional level depending on the mismatch between species extinctions and interaction extinctions. Situations of interaction surplus occur whenever interactions are lost at a lower rate than species along the disturbance gradient. This is expected, for example, when species 'rewire' their ecological links in absence of missing partners (Pires *et al.* 2014). Situations of interaction deficit are also frequent because they relate to the loss of species functionality that precedes species extinction. Reduced abundances of super-generalist species due to logging (trees) or hunting (mega-fauna vertebrates) may cause ecological extinction and trigger the loss of multiple interactions, resulting in interaction deficits and a sizeable interactions–extinction debt.

Therefore, although most previous studies on the biodiversity–ecosystem functioning paradigm have focused exclusively on species richness, our novel analytical approach reveals the relevance of considering the species interaction balance as a critical indicator of ecosystem health (see Table S1, supporting information for a summary of examples). To ensure the long-term provision of ecosystem services that depend upon biodiversity, the greatest attention should be focused on those components of biodiversity, such as species interactions, that can be affected by the new scenarios emerging in a changing world. Anthropogenic impacts are the most evident causes of biodiversity loss, but other causes can also be at work. The consequence of species interactions loss for biodiversity is just an emerging field. Box 3 outlines future avenues and issues for research on the consequences of species interaction loss for biodiversity reductions. Thus, the focus on the health of biotic interactions provides a deeper, process-oriented understanding of the functional consequences of biodiversity in a changing world. Using interaction

Box 3: Key issues for future research

Drivers for change in the interaction balance

1. What are the main drivers of interaction debts?
2. How do changes in species diversity influence changes in the diversity of interactions and their balance?

Interaction network structure

1. How does the loss of interactions impact the structure of interaction networks?
2. Are different types of interaction loss (surplus vs. deficit) associated with different types of interactions (e.g. mutualistic vs. antagonistic)?

Ecological services

1. What is the impact of losing different types of interactions (i. e. additive, keystone, redundant) upon ecological services?
2. To what extent ecological services depend on interaction balance?

losses as early warning signals of critical transitions is necessary to identify and quantify extinction debt and would allow us detecting early on-time thresholds of habitat loss from which collapse of ecosystem functions is imminent.

Acknowledgements

Four workshops that led to this publication were organized with financial support provided by Programa Iberoamericano de Ciencia y Tecnología para el Desarrollo (CYTED Project 409AC0369). AV-B thanks to Alejandro de Avila and co-workers for facilities during the workshop held in the Botanical Garden of the Centro Cultural Santo Domingo, Oaxaca, Mexico. MBG thanks the funding received from the Spanish MEC (CGL2011-13456-E). PJ was supported by a Junta de Andalucía Excellence Grant (RNM-5731), as well as a Severo Ochoa Excellence Award from the Ministerio de Economía y Competitividad (SEV-2012-0262). RM thanks the funding support from FONDECYT 1120155. MG received a fellowship from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP). Marc Johnson, Angela Moles and one anonymous reviewer greatly improved the manuscript with their comments.

Authorship

RZ, MAA, MBG and AV-B organized the workshops in Granada (Spain), Bariloche (Argentina), Jaca (Spain) and Oaxaca (Mexico), respectively. All the authors attended the workshops, outlined the manuscript and contributed substantially to its writing. AC, JMG and PJ prepared all figures.

References

- Aizen, M., Sabatino, M. & Tylianakis, J.M. (2012) Specialization and rarity predict nonrandom loss of interactions from mutualist networks. *Science*, **335**, 1486–1489.
- Améztegui, A., Brotons, L. & Coll, L. (2010) Land-use changes as major drivers of mountain pine (*Pinus uncinata* Ram.) expansion in the Pyrenees. *Global Ecology and Biogeography*, **19**, 632–641.
- Anderson, S.H., Kelly, D., Ladley, J.L., Molloy, S. & Terry, J. (2011) Cascading effects of bird functional extinction reduce pollination and plant density. *Science*, **331**, 1068–1071.

- Arroyo, J. & Dafni, A. (1995) Variations in habitat, season, flower traits and pollinators in dimorphic *Narcissus tazetta* L. (Amaryllidaceae) in Israel. *New Phytologist*, **129**, 135–145.
- Aslan, C.E., Zavaleta, E.S., Tershy, B. & Croll, D. (2013) Mutualism disruption threatens global plant biodiversity: a systematic review. *PLoS ONE*, **8**, e66993.
- Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.-S., Nakashizuka, T., Raffaelli, D. et al. (2006) Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters*, **9**, 1146–1156.
- Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O., Schwartz, B., Quental, T.B. et al. (2011) Has the Earth's sixth mass extinction already arrived? *Nature*, **471**, 51–57.
- Beaune, D., Fruth, B., Bollache, L., Hohmann, G. & Bretagnolle, F. (2013) Doom of the elephant-dependent trees in a Congo tropical forest. *Forest Ecology and Management*, **295**, 109–117.
- Breitbart, N., Tillmann, S., Schleuning, M., Grunewald, C., Laube, I., Stefan-Dewenter, I. et al. (2012) Influence of habitat complexity and landscape configuration on pollination and seed-dispersal interactions of wild cherry trees. *Oecologia*, **168**, 425–437.
- Brys, R. & Jacquemyn, H. (2012) Effects of human-mediated pollinator impoverishment on floral traits and mating patterns in a short-lived herb: an experimental approach. *Functional Ecology*, **26**, 189–197.
- Bueno, R.S., Guevara, R., Ribeiro, M.C., Culot, L., Bufalo, L.S. & Galetti, M. (2013) Functional redundancy and complementarities of seed dispersal by the last neotropical megafrugivores. *PLoS ONE*, **8**, e56252.
- Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P. et al. (2012) Biodiversity loss and its importance on humanity. *Nature*, **486**, 59–67.
- Castillo, L.J.P., Verdú, M. & Valiente-Banuet, A. (2010) Neighborhood phylodiversity affects plant performance. *Ecology*, **91**, 3656–3663.
- Connell, J.H. & Slatyer, R.O. (1977) Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist*, **982**, 1119–1144.
- Díaz, S., Purvis, A., Cornelissen, J.H.C., Mace, G.M., Donoghue, M.J., Ewers, R.M. et al. (2013) Functional traits, the phylogeny of function, and ecosystem service vulnerability. *Ecology and Evolution*, **3**, 2958–2975.
- Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B. & Collen, B. (2014) Defaunation in the Anthropocene. *Science (New York, NY)*, **345**, 401–406.
- Dunn, R.R., Harris, N.C., Colwell, R.K., Koh, L.P. & Sodhi, N.S. (2009) The sixth mass coextinction: are most endangered species parasites and mutualists? *Proceedings of the Royal Society B: Biological Sciences*, **276**, 3037–3045.
- Fleming, T.H., Sahley, C.T., Holland, J.N., Nason, J.D. & Hamrick, J.L. (2001) Sonoran Desert columnar cacti and the evolution of generalized pollination systems. *Ecological Monographs*, **71**, 511–530.
- Fragoso, J.M.V. (1997) Tapir-generated seed shadows: scale-dependent patchiness in the Amazon rain forest. *Journal of Ecology*, **85**, 519–529.
- Fründ, J., Dormann, C.F., Holzschuh, A. & Tschirntke, T. (2013) Bee diversity effects on pollination depend on functional complementarity and niche shifts. *Ecology*, **94**, 2042–2054.
- Galetti, M., Donatti, C.I., Pires, A.S., Guimarães, J.R. & Jordano, P. (2006) Seed survival and dispersal of an endemic Atlantic forest palm: the combined effects of defaunation and forest fragmentation. *Botanical Journal of the Linnean Society*, **151**, 141–149.
- Galetti, M., Guevara, R., Córtes, M.C., Fadini, R., Von Matter, S., Leite, A.B. et al. (2013) Functional extinction of birds drives rapid evolutionary changes in seed size. *Science*, **340**, 1086–1090.
- García, M.B., Antor, R.J. & Espadaler, X. (1995) Ant pollination of the palaeoendemic dioecious *Borderia pyrenaica* (Dioscoreaceae). *Plant Systematics and Evolution*, **198**, 17–27.
- García, D., Martínez, D., Herrera, J.M. & Morales, J.M. (2013) Functional heterogeneity in a plant-frugivore assemblage enhances seed dispersal resilience to habitat loss. *Ecography*, **36**, 197–208.
- Gómez, J.M. & Zamora, R. (1999) Generalization vs. Specialization in the pollination system of *Hormatophylla spinosa* (Cruciferae). *Ecology*, **80**, 796–805.
- González-Varo, J.P., Arroyo, J. & Aparicio, A. (2009) Effects of fragmentation on pollinator assemblage, pollen limitation and seed production of Mediterranean myrtle (*Myrtus communis*). *Biological Conservation*, **142**, 1058–1065.
- González-Varo, J.P., Albaladejo, R.G., Aparicio, A. & Arroyo, J. (2010) Linking genetic diversity, mating patterns and progeny performance in fragmented populations of a Mediterranean shrub. *Journal of Applied Ecology*, **47**, 1242–1252.
- Greenwood, J.J. (1985) Frequency-dependent selection by seed-predators. *Oikos*, **44**, 195–210.
- Guimarães, P.R. Jr, Galetti, M. & Jordano, P. (2008) Seed Dispersal Anachronisms: rethinking the fruits extinct megafauna ate. *PLoS ONE*, **3**, e1745.
- Guimarães, P.R. Jr, Jordano, P. & Thompson, J.N. (2011) Evolution and coevolution in mutualistic networks. *Ecology Letters*, **14**, 877–885.
- Hagen, M., Kissling, W.D., Rasmussen, C., Marcus, A.M., De Aguiar, M.A.M., Brown, L.E. et al. (2012) Biodiversity, species interactions and ecological networks in a fragmented world. *Advances in Ecological Research*, **46**, 89–210.
- Haurez, B., Petre, C.-A. & Doucet, J.-L. (2013) Impacts of logging and hunting on western lowland gorilla (*Gorilla gorilla gorilla*) populations and consequences for forest regeneration. A review. *Biotechnology, Agronomy, Society and Environment*, **17**, 364–372.
- He, F. & Hubbell, S.P. (2011) Species–area relationships always overestimate extinction rates from habitat loss. *Nature*, **473**, 368–371.
- Helfield, J.M. & Naiman, R.J. (2006) Keystone interactions: salmon and bear in riparian forests of Alaska. *Ecosystems*, **9**, 167–180.
- Holland, J.N. & DeAngelis, D.L. (2010) A consumer–resource approach to the density-dependent population dynamics of mutualism. *Ecology*, **91**, 1286–1295.
- Ings, T.C., Montoya, J.M., Bascompte, J., Blüthgen, N., Brown, L., Dormann, C.F. et al. (2009) Ecological networks – beyond food webs. *Journal of Animal Ecology*, **78**, 253–269.
- Jacquemyn, H., De Meester, L., Jongejans, E. & Honnay, O. (2012) Evolutionary changes in plant reproductive traits following habitat fragmentation and their consequences for population fitness. *Journal of Ecology*, **100**, 76–87.
- Jansen, P.A., Hirsch, B.T., Emsens, W.J., Zamora-Gutierrez, V., Wikelski, M. & Kays, R. (2012) Thieving rodents as substitute dispersers of megafaunal seeds. *Proceedings of the National Academy of Sciences, USA*, **109**, 12610–12615.
- Janzen, D.H. (1974) The deflowering of Central America. *Natural History of New York*, **83**, 48–53.
- Janzen, D.H. (2001) Latent extinction—the living dead. *Encyclopedia of Biodiversity*, **3**, 689–699. Academic Press.
- Kaiser-Bunbury, C.N., Muff, S., Memmott, J., Müller, C. & Cafish, A. (2010) The robustness of pollination networks to the loss of species and interactions, a quantitative approach incorporating pollinator behaviour. *Ecology Letters*, **13**, 442–452.
- Koh, L.P., Dunn, R.R., Sodhi, N.S., Colwell, R.K., Proctor, H.C. & Smith, V.S. (2004) Species coextinctions and the biodiversity crisis. *Science*, **305**, 1632–1634.
- Kremen, C., Williams, N.M., Aizen, M.A., Gemmill-Herren, B., LeBuhn, G., Minckley, R. et al. (2007) Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecology Letters*, **10**, 299–314.
- Lawton, J.H. & Brown, V.K. (1993). Redundancy in ecosystems. *Biodiversity and Ecosystem Function* (eds E. D. Schulze & H. A. Mooney), pp. 255–270. Springer Verlag, New York.
- Lekberg, Y., Gibbons, S.M., Rosendahl, S. & Ramsey, P.W. (2013) Severe plant invasions can increase mycorrhizal fungal abundance and diversity. *ISME Journal*, **7**, 1424–1433.
- Macleán, I.M.D. & Wilson, R.J. (2011) Recent ecological responses to climate change support predictions of high extinction risk. *Proceedings of the National Academy of Science, USA*, **108**, 12337–12342.
- May, R.M. (1972) Will a large complex system be stable? *Nature*, **38**, 413–414.
- McConkey, K.R. & Drake, D.R. (2006) Flying foxes cease to function as seed dispersers long before they become rare. *Ecology*, **87**, 271–276.
- Mitchell, R.J., Flanagan, R.J., Brown, B.J., Waser, N.M. & Karron, J.D. (2009) New frontiers in competition for pollination. *Annals of Botany*, **103**, 1403–1413.
- Muriá, M., Espinoza, C., Bustamante, R.O., Marín, V.H. & Medel, R. (2010) Does human-induced habitat transformation modify pollinator-mediated selection? a case study in *Viola portalesia* (Violaceae). *Oecologia*, **163**, 153–162.
- Novaro, A.J., Funes, M.C. & Walker, R.S. (2000) Ecological extinction of native prey of a carnivore assemblage in Argentine Patagonia. *Biological Conservation*, **92**, 25–33.
- Olf, H. & Ritchie, M.E. (1998) Effects of herbivores on grassland plant diversity. *Trends in Ecology and Evolution*, **13**, 261–265.

- Peres, C.A., Baider, C., Zuidema, P.A., Wadt, L.H.O., Kainer, K.A., Gomes-Silva, D.A.P. *et al.* (2003) Demographic threats to the sustainability of Brazil nut exploitation. *Science*, **302**, 2112–2114.
- Pérez-Barrales, R. & Arroyo, J. (2010) Pollinator shifts and the loss of style polymorphism in *Narcissus papyraceus* (Amaryllidaceae). *Journal of Evolutionary Biology*, **23**, 1117–1128.
- Pérez-Barrales, R., Vargas, P. & Arroyo, J. (2006) New evidence for the Darwinian hypothesis of heterostyly: breeding systems and pollinators in *Narcissus* sect. *Apodanthi*. *New Phytologist*, **171**, 553–567.
- Pimm, S.L., Lawton, J.H. & Cohen, J.E. (1991) Food webs patterns and their consequences. *Nature*, **350**, 669–674.
- Pires, M.M., Galetti, M., Donatti, C.I., Pizo, M.A., Dirzo, R. & Guimarães, P.R. (2014) Reconstructing past ecological networks: the reconfiguration of seed-dispersal interactions after megafaunal extinction. *Oecologia*, **175**, 1247–1256.
- Quental, T.B. & Marshall, C.R. (2013) How the Red Queen drives terrestrial mammals to extinction. *Science*, **341**, 290–292.
- Redford, K.H. (1992) The empty forest. *BioScience*, **42**, 412–422.
- Rezende, E.L., Lavabre, J.E., Guimarães, P.R., Jordano, P. & Bascompte, J. (2007) Non-random coextinctions in phylogenetically structured mutualistic networks. *Nature*, **448**, 925–928.
- Ripple, W.J. & Beschta, R.L. (2006) Linking wolves to willows via risk-sensitive foraging by ungulates in the northern Yellowstone ecosystem. *Forest Ecology and Management*, **230**, 96–106.
- Rooney, T.P. (1997) Escaping herbivory: refuge effects on the morphology and shoot demography of the clonal forest herb *Maianthemum canadense*. *Journal of the Torrey Botanical Society*, **124**, 280–285.
- Sabatino, M., Maceira, N. & Aizen, M.A. (2010) Direct effects of habitat area on interaction diversity in pollination webs. *Ecological Applications*, **20**, 1491–1497.
- Säterberg, T., Stellan, S. & Ebenman, B. (2013) High frequency of functional extinctions in ecological networks. *Nature*, **499**, 468–470.
- Stouffer, D.B., Cirtwill, A.R. & Bascompte, J. (2014) How exotic plants integrate into pollination networks. *Journal of Ecology*, DOI: 10.1111/1365-2745.12310.
- Tilman, D., May, R.M., Lehman, C.L. & Nowak, M.A. (1994) Habitat destruction and the extinction debt. *Nature*, **371**, 65–66.
- Traveset, A. & Riera, N. (2005) Disruption of a plant-lizard seed dispersal system and its ecological effects on a threatened endemic plant in the Balearic Islands. *Conservation Biology*, **19**, 422–431.
- Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008) Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, **11**, 1351–1366.
- Tylianakis, J.M., Lalibert, E., Nielsen, A. & Bascompte, J. (2010) Conservation of species interaction networks. *Biological Conservation*, **143**, 2270–2279.
- Underwood, N. & Halpern, S. (2012) Insect herbivores, density dependence, and the performance of the perennial herb *Solanum carolinense*. *Ecology*, **93**, 1026–1035.
- Valiente-Banuet, A. & Verdú, M. (2013) Human impacts on multiple ecological networks act synergistically to drive ecosystem collapse. *Frontiers in Ecology and the Environment*, **11**, 408–413.
- Verdú, M. & Valiente-Banuet, A. (2008) The nested assembly of plant facilitation networks prevents species extinctions. *American Naturalist*, **172**, 751–760.
- Verdú, M., Rey, P., Alcántara, J.M., Siles, G. & Valiente-Banuet, A. (2009) Phylogenetic signatures of facilitation and competition in successional communities. *Journal of Ecology*, **97**, 1171–1180.
- Visser, M.E. & Holleman, L.J.M. (2001) Warmer springs disrupt the synchrony of oak and winter moth phenology. *Proceedings of the Royal Society of London B*, **268**, 289–294.
- Wearn, O.R., Reuman, D.C. & Ewers, R.M. (2012) Extinction debt and windows of conservation opportunity in the Brazilian Amazon. *Science*, **337**, 228–232.
- Weiblen, G.D. (2002) How to be a fig wasp. *Annual Review of Entomology*, **47**, 299–330.
- Wilkie, D.S., Bennett, E.L., Peres, C.A. & Cunningham, A.A. (2011) The empty forest revisited. *Annals of the New York Academy of Sciences*, **1223**, 120–128.

Received 19 February 2014; accepted 6 October 2014

Handling Editor: Marc Johnson

Supporting Information

Additional Supporting information may be found in the online version of this article:

Table S1. Summary of biotic interactions considering interaction balance and effects on functionality.