

LETTER

How specialised must natural enemies be to facilitate coexistence among plants?

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Abstract

The Janzen–Connell hypothesis proposes that plant interactions with host-specific antagonists can impair the fitness of locally abundant species and thereby facilitate coexistence. However, insects and pathogens that associate with multiple hosts may mediate exclusion rather than coexistence. We employ a simulation model to examine the effect of enemy host breadth on plant species richness and defence community structure, and to assess expected diversity maintenance in example systems. Only models in which plant enemy similarity declines rapidly with defence similarity support greater species richness than models of neutral drift. In contrast, a wide range of enemy host breadths result in spatial dispersion of defence traits, at both landscape and local scales, indicating that enemy-mediated competition may increase defence-trait diversity without enhancing species richness. Nevertheless, insect and pathogen host associations in Panama and Papua New Guinea demonstrate a potential to enhance plant species richness and defence-trait diversity comparable to strictly specialised enemies.

Keywords

Coexistence, community structure, frequency dependence, host specialisation, Janzen–Connell, plant–enemy interactions, species richness, tropical forest.

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INTRODUCTION

How large numbers of plant species manage to co-exist in the face of intense competition for light, water and other shared resources remains a fundamental challenge to community ecology (Wright 2002; Silvertown 2004). A now-classical hypothesis put forth independently by Janzen (1970) and Connell (1971) proposes that plants fail to recruit in the neighbourhood of conspecific adults as a result of attack by specialised natural enemies, such as insects or pathogens, that respond either to the presence of adult plants or to the density of offspring of their host species. This mechanism is thought to limit the abundance of any given species, and thereby facilitate coexistence among plants.

A considerable amount of evidence has accrued in the last 40 years in support of the predictions of Janzen and Connell, namely that offspring fail to survive at high densities or in the vicinity of conspecific adults in tropical forests (e.g. Wills *et al.* 1997; Webb & Peart 1999; Harms *et al.* 2000; HilleRisLambers *et al.* 2002; Comita *et al.* 2010; Terborgh 2012). Yet, recent large-scale community surveys suggest that within at least some communities of both insect herbivores (Basset 1992; Odegaard *et al.* 2000, 2005; Novotny *et al.* 2002, 2010) and fungal pathogens (Gilbert 2005; Gilbert & Webb 2007; Liu *et al.* 2012), enemies seldom specialise on a single host, but rather associate with a range of often closely related species. In addition, recruitment patterns consistent with the expectations of Janzen and Connell are not restricted to the tropics (Johnson *et al.* 2012), despite some suggestions that host specificity declines with latitude (Dyer *et al.* 2007). More broadly, knowledge of how specialised enemies are, and how large of an effect specialised enemies have on host fitness as compared with their more generalist counterparts, is rather limited. Shared natural enemies may result in coexistence or competitive exclusion depending on the degree to which competitors partition niche space defined by antagonists (Bever 2003; Chesson & Kuang

2008). Hence, it remains unclear whether plants differ in their interactions with enemies sufficiently to facilitate the maintenance of diversity in tropical forests (Freckleton & Lewis 2006) or elsewhere. Are plant antagonists specialised enough to facilitate coexistence? How specialised must they be?

Even if natural enemies are not specialised enough to foster coexistence of competing plant species, they may still influence the phylogenetic or defence trait composition in plant communities. The degree to which plant species share herbivores (Novotny *et al.* 2002, 2010; Odegaard *et al.* 2005) or pathogens (Gilbert & Webb 2007; Liu *et al.* 2012) is broadly associated with plant phylogeny, most likely as a result of conservatism of host use-determining traits at deep scales of phylogeny (Wink 2003; Barrett & Heil 2012). As a result, the exclusion of related heterospecific individuals through competition mediated by shared enemies (Holt 1977) may be partially responsible for observations of phylogenetically even ('overdispersed' *sensu* Cavender-Bares *et al.* 2004) species assemblages at small spatial scales (Webb *et al.* 2006; Bagchi *et al.* 2010; Metz *et al.* 2010). On the other hand, detailed investigations of *Asclepias* milkweeds (Agrawal & Fishbein 2006) and the tropical tree genera *Bursera* (Becerra 1997) and *Inga* (Kursar *et al.* 2009) suggest that plant defences can be quite evolutionarily labile at finer scales of phylogeny, such as within a genus. Furthermore, communities of co-occurring *Bursera* (Becerra 2007) and *Inga* (Kursar *et al.* 2009) appear to exhibit a more even distribution of defences than by chance. These findings suggest that density-responsive insects and pathogens increase the diversity of the plant community with respect to defence traits, and potentially increase plant species richness in the process. Furthermore, by allowing phenotypically distinct plants to escape the enemy load of neighbouring heterospecifics, nonspecialist enemies may promote divergence in defence among closely related species, thus linking the Janzen–Connell (J–C) mechanism of diversity maintenance with the role of enemies in promoting plant lineage diversification posited by Ehrlich & Raven (1964).

Here, we consider quantitatively a modified version of the strict J-C hypothesis, in which natural enemies of intermediate host specificity shape the spatial organisation of plants with respect to defence and thereby contribute to diversification and the maintenance of species richness. If offspring mortality is dependent on distance to conspecific adults, as well as adults belonging to species with which the offspring is likely to share enemies, subsequent generations ought to exhibit an even distribution of adults with respect to plant defence similarity. The tendency for such trait dispersion should be stronger if enemies are not strict specialists. Substantial maintenance of species diversity may accompany this pattern of spatial dispersion in traits, despite the lack of strict specialisation allowing for a simple division of limiting or regulating factors (Levin 1970; Meszina *et al.* 2006) that would enable the possibility of stable coexistence. Webb *et al.* (2006), and later other authors (Bagchi *et al.* 2010; Dyer *et al.* 2010; Metz *et al.* 2010) discussed a similar generalisation of the J-C.

We explore this modified J-C hypothesis using a simulation model. We begin with Adler & Muller-Landau's (2005) model of the J-C mechanism and relax its assumption that plant antagonists specialise on a single host species. We assume that the proportion of shared enemies between two plant species is a function of the plants' defence trait similarity. We then manipulate the shape of this function to reflect alternative models of enemy host breadth, ranging from a model that approaches the J-C model, to one in which antagonists are highly generalist (Fig. 1a). We examine not only the number of plant species maintained in the community at equilibrium as a function of this relationship, but also its influence on the spatial structure of defence traits in the community. We also use three case studies of insects and pathogens in Panama and Papua New Guinea to assess expected community structure and diversity maintenance from the modified J-C hypothesis in those systems. Some prior theoretical exploration of coexistence implications of non-specialist enemies exists (Bever 2003; Chesson & Kuang 2008). Here, we specifically consider the J-C mechanism in a stochastic, spatially-explicit framework that permits an assessment of dynamic diversity maintenance compared with a neutral model and of potential diversity maintenance in example communities.

We show that only scenarios in which plant enemy similarity declines rapidly as a function of pairwise defensive trait distance support greater species richness than models of neutral drift. Nonetheless, a wide range of variation in enemy host specificity results in the dispersion of defensively similar plant species, both at the scale of the landscape and the local neighbourhood, indicating that enemy-mediated competition may increase defence trait diversity without necessarily enhancing species richness. Indeed, the strongest trait dispersion seems to occur at intermediate host specificities, where diversity is no higher than in a neutral model. Finally, in exploring predictions of the model using observed host ranges, we find that studies of herbivorous beetles (Odegaard *et al.* 2005) and pathogenic fungi (Gilbert & Webb 2007) in Panama, as well as a large-scale survey of caterpillars in Papua New Guinea (Novotny *et al.* 2010), demonstrate sufficiently narrow host ranges to substantially enhance both plant species richness and the diversity of plant defence traits in those communities.

THE SIMULATION MODEL

Each species in a regional species pool of K species is assigned a random position in two-dimensional space used here to represent

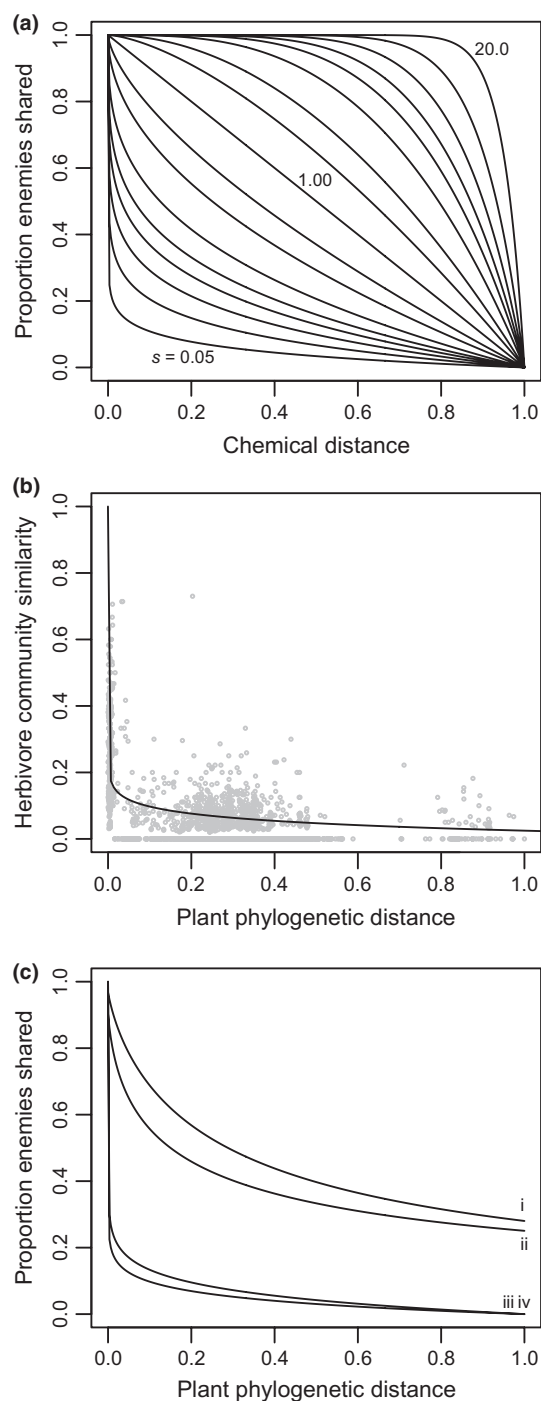


Figure 1 Theoretical and empirical relationships between plant enemy similarity and defence trait or phylogenetic distance. (a) Proportion of enemies shared vs. simulated trait distance for 17 values of the defence shape parameter s of the function in eqn 1. (b) Jaccard index of Lepidopteran herbivore similarity vs. plant phylogenetic distance in Papua New Guinea (Novotny *et al.* 2010). (c) Empirical curves pertaining to (1) pathogenic fungi, nursery, (2) moist forest, Panama (Gilbert & Webb 2007), (3) Coleopteran herbivores, wet forest and (4) dry forest, Panama (Odegaard *et al.* 2005).

secondary compounds and other traits that may influence enemy host use. We refer to this trait space as 'defence' space and the Euclidean distance between species pairs, ρ , as 'defence' distance.

These trait distances exhibit a normal distribution and are scaled so that $\rho_{\max} = 1$.

The model follows the fates of a fixed number N of adult plants in a two-dimensional landscape of L by L metres. We employ a torus to eliminate edge effects. The initial community is assembled by selecting N individuals' starting positions randomly and uniformly. Species identities are assigned by selecting at random from a regional pool of species with equal probability with replacement. The J-C recruitment process is then reflected in a series of death and replacement events, in which a randomly chosen adult dies, and potential offspring undergo recruitment trials until one reaches adulthood and is added to the community to replace the dying individual (not necessarily at the same location). These dynamics keep the total number of adults in the community fixed.

In each death and replacement event, there is a probability μ that the replacing individual is an immigrant offspring. In this case, the location of the offspring is chosen randomly and uniformly, and its species identity chosen with equal probability from the regional species pool. With probability $1 - \mu$, an adult within the community is chosen at random to produce a single offspring, which disperses in a uniformly random direction a distance r chosen from the exponential probability density function $f(r)$, with mean seed dispersal distance σ :

$$f(r) = (1/\sigma)e^{-r/\sigma} \quad (1)$$

The probability that any offspring survives after dispersal depends on the local density of natural enemies. In the model of Adler & Muller-Landau (2005), enemy density is a function of distance to conspecific adults. In our model, enemy density is a function of distance to each adult in the landscape, weighted by the probability that the offspring shares an enemy with the species of that adult. The proportion of enemies shared between an offspring of plant species i and an adult of species j is a function of their defence distance ρ :

$$g(\rho) = 1 - \rho_{ij}^s, \quad (2)$$

where s is the shape parameter describing the relationship between defence distance and shared enemies (Fig. 1a). Furthermore, the probability of an enemy dispersing to the site x of the offspring is a function of the distance between the offspring and each adult k in the landscape, $r_k(x) = d(x_k, x)$:

$$b(r_k(x)) = [1/(2\pi\alpha)]\exp(-r_k(x)/\alpha) \quad (3)$$

where α is the mean enemy dispersal distance. Thus, the number of enemies of species i at site x , $H_i(x)$, is

$$H_i(x) = \sum_k b(r_k(x))g(\rho_{ij(k)}), \quad (4)$$

where $\rho_{ij(k)}$ is the defence distance between species i and the species j to which individual k belongs. The probability that an offspring of species i survives at location x is

$$P_i(x) = 1/(1 + \beta NH_i(x)), \quad (5)$$

where β is a scaling parameter that describes the strength of enemy attack and N is the number of adults. If an offspring does not survive, a new adult is chosen to produce an offspring and this process is repeated until an offspring survives. If an offspring survives, it immediately becomes an adult and another death and replacement event commences, beginning with the mortality of a new randomly chosen adult.

We consider a range of values for the defence shape parameter, s , that extend from a rapidly declining proportion of shared enemies as a function of plant trait distance (when $s = 1/20 = 0.05$), to a linear decline (when $s = 1$), to a convex relationship in which most plant species pairs share a high proportion of natural enemies ($s = 20$; Fig. 1a). In addition to these model variants that account for the influence of plant traits, we consider three simplified models in which traits are ignored. In the strict J-C model, the number of enemies, and ultimately offspring survival, depends only on distance to conspecific adults. In the Generalist model, offspring survival depends on distance to all adults, species identity notwithstanding. Finally, we consider a neutral model (Hubbell 2001) in which recruitment is not influenced by enemies, leaving species richness to be governed by the opposing forces of demographic drift and immigration from the regional species pool.

Asymmetrical resource competition in plants can make offspring establishment directly below an adult impossible. To incorporate the influence of adult shading or other resource competition on seedling establishment and potential diversity-maintenance through the J-C mechanism, we incorporated a threshold distance R below which establishment cannot occur:

$$f(r) = 0 \quad \text{if } r \leq R \quad (6)$$

$$f(r) = (1/\sigma)e^{-r/\sigma} \quad \text{if } r > R \quad (7)$$

The threshold parameter has the effect of imposing spatial structure on the distribution of adults in the community, ranging from strongly clustered (at $R = 0$ m) to evenly dispersed (at $R \geq 3$ m).

To allow us to maximally differentiate diversity maintained by different values of s , we used the combination of offspring and enemy dispersal distances ($\alpha = \sigma = 5$ m) that resulted in substantially more species than the neutral case in the strict J-C simulation according to Adler & Muller-Landau (2005) and our own explorations. We explored a range of threshold distance (R) values, and, because the mechanism is mediated by survival, three different functional forms relating offspring survival to enemy density (see Table 1). Figs 2–4 show results for $R = 3$ and survival as in eqn 4, but key results are robust over R values and survival functions considered (Figures S1–S4 in Supporting Information).

We employed pairwise distance metrics to examine the influence of s on defence trait community structure as well as the relationship between defence trait diversity and species richness. We calculated the mean pairwise defence distance of all species found on the landscape compared to that expected from a random sample of an equal number of species from the regional species pool (Webb 2000) as well as the mean pairwise defence distance within the neighbourhood < 5 m of each individual on the landscape. In addition, we calculated the mean distance to the centre of our two-dimensional defence space for all individuals in the landscape to understand the degree to which species on the landscape represent the outer boundaries of trait variation in the regional species pool and calculated the probability of immigration success as a function of trait distance to the most abundant resident.

Three studies have examined the relationship between the proportion of enemies shared between species of plants and the plants' phylogenetic relationships. Odegaard *et al.* (2005) investigated host use among 1174 species of Coleopteran herbivores of 50 and 52 tree species in a wet and dry tropical forest, respectively, in central Panama. Also working in Panama, Gilbert & Webb (2007) analysed

Table 1 Variables, parameters and functions in the simulation

Parameters	Values
L , length/width of the landscape	200 m
N , total population size	400
K , number of species in regional species pool	1000
μ , probability of immigration	$0.001(N)$
β , strength of frequency dependence	25, 2.5
α , mean enemy dispersal distance	5 m
σ , mean offspring dispersal distance	5 m
R , threshold distance for offspring survival	0–5 m
ρ , defence trait distance between species	0–1
s , shape of the proportion of enemies shared as a function of defense trait distance	0.05, 0.10, 0.15, 0.20, 0.25, 0.33, 0.50, 0.67, 1.00, 1.50, 2.00, 3.00, 4.00, 5.00, 6.67, 10.00, or 20.00
Observed plant-enemy relationship	Function
P_{wets} , Coleoptera in Panama wet forest (Odegaard <i>et al.</i> 2005)	$1 - \rho^{0.0446}$
P_{dry} , Coleoptera in Panama dry forest (Odegaard <i>et al.</i> 2005)	$1 - \rho^{0.0622}$
P_{Lep} , Lepidoptera in Papua New Guinea (Novotny <i>et al.</i> 2010)	$1 - \rho^{0.0336}$
P_{log} , Lepidoptera in Papua New Guinea, treating log(plant phylogeny) (Novotny <i>et al.</i> 2010)	$0.3966 - \rho(0.4407)$
$P_{nursery}$, Fungal pathogens in Panama (Gilbert & Webb 2007)	$\text{logit}(S) = 3.4096 - 1.7562(\log_{10}(1 + \rho*300))$
$P_{forests}$, Fungal pathogens in Panama (Gilbert & Webb 2007)	$\text{logit}(S) = 2.2327 - 1.3428(\log_{10}(1 + \rho*300))$
Functional forms	
Survival function $P(H)$	$1/(1 + \beta NH)$, $1/(1 + \beta N \log(1+H))$, $1/(1 + (\beta NH)^2)$

Gilbert & Webb (2007) defined shared pathogens with the logit function: $P = \exp(\text{logit}(S)) / [1 + \exp(\text{logit}(S))]$.

the probability that a fungal pathogen would infect a host plant as a function of the phylogenetic distance between the host and the plant species from which the pathogen was isolated. These data included 53 species of tissue-killing fungi and 36 plant species (Gilbert & Webb 2007). Finally, in a large-scale, community-wide study of 1490 insect herbivore species in 11 feeding guilds, Novotny *et al.* (2010) examined the phylogenetic relationships of the 88 host plant species utilised by 572 species of leaf-feeding caterpillars in Papua New Guinea. To examine the potential for the natural enemies in each of these studies to facilitate coexistence within their respective tree communities via the J-C mechanism, we parameterised our simulation model with the curves in each study reflecting the proportion of enemies shared as a function of phylogenetic distance, a pattern shaped by species differences in secondary chemistry and other defensive traits represented in our theoretical model by the parameter ρ (Fig. 1b and c; Table 1). We used these studies to explore the implications of the shape parameter s for diversity maintenance and defensive trait similarity in these systems, but did not incorporate other parameters (e.g. enemy dispersal, seed-dispersal distances) from these communities. Nevertheless, we were able to compare the potential for diversity maintenance in these three communities to that maintained by strict J-C, generalist, and neutral models under conditions in which the strict J-C mechanism is an effective mechanism of coexistence.

Simulation code was written in R (R Development Core Team 2011) and is available in Appendix S2. We simulated 400 adults in a 4 ha local community with a regional species pool of $K = 1000$ species. Plotted results are based on 20 different communities, each the state achieved after stochastic simulation of 400 000 adult deaths, or 1000 generations, beginning from a community randomly generated from the regional species pool.

RESULTS

Offspring of rare species encounter a more favourable landscape upon dispersal when s is low, and host specificity high, than do off-

spring of abundant species (Fig. 2). This advantage erodes as s increases from 0.10 to 1.00, as the offspring even of a rare species are likely to disperse to a neighbourhood teeming with enemies they share with heterospecific adults (Fig. 2h).

As shown in Fig. 3a, increasing the shape parameter, and thereby increasing the proportion of shared enemies over greater defence trait distances (Fig. 1a), results in reduced species richness relative to the strict J-C model. Models in which s is small ($0.05 \leq s \leq 1.00$) enhance species richness relative to the neutral case, whereas models in which $1.00 \leq s \leq 5.00$, suppress species richness relative to that maintained under neutral drift with immigration. A model in which all enemies are generalists supports no more than the number of species maintained by neutral drift and immigration. Models in which $s \geq 6.67$ behave similarly to the generalist and neutral models. The proportion of enemies shared by most plant species pairs must be low ($s < 1$) in order to confer a rare species advantage (see Figure S5) and thereby slow the loss of diversity through ecological drift. Relative diversity maintenance is robust to the threshold distance R (Figure S1) as well as the function relating offspring survival to enemy density (Figures S3 and S4) with the exception that when the threshold distance $R = 0$, the resulting spatial clustering of adult plants allows even generalist enemies to maintain 20% more plant species than neutral drift, and does not suppress species richness in communities with $1.00 \leq s \leq 5.00$.

Nearly all models we considered resulted in highly non-random trait structure in the plant community, whether measured at the scale of the landscape (Fig. 3b) or the immediate neighbourhood surrounding individual adults (Fig. 3c). For most values of s , the mean defence distance between species in the landscape differed greatly from that in null communities (Fig. 3b). Only the true J-C model and models with exceedingly generalist enemies ($s > 6.67$) exhibited random species composition with respect to defence. The strength of exclusion of defensively similar individuals within the immediate neighbourhood (5 m) of adults mirrored the degree of landscape-wide trait structure with the exception of the true J-C

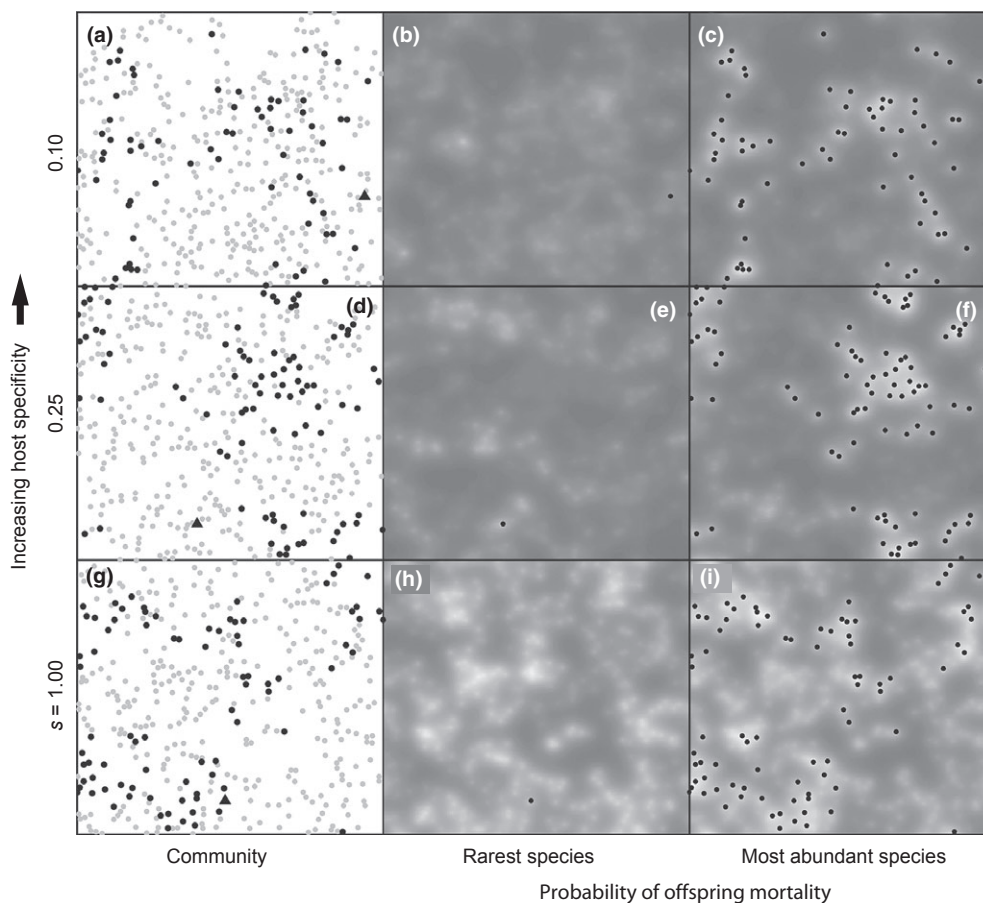


Figure 2 Community structure and the probability of offspring mortality of rare and abundant species. Community structure is shown after 50 000 adult deaths for simulations in which $s = 0.1, 0.25$ and 1 respectively. The left panel shows the adult community in grey, with the individuals of the rarest species represented by triangles and those of the most abundant by black circles. In the centre and right panels, prevalence of enemies of the rarest and most abundant species are shown respectively as a heat map (low prevalence = dark, high = light) with individuals of the species in question indicated with circles. Differences in enemy prevalence in areas inhabited by neither species are a result of differences in defence traits and the composition of the rest of the community; this is most visually apparent between panels (e) and (f).

model. The J-C model results in greater mean neighbourhood trait distances than models in which enemies are highly generalist ($3.00 \leq s \leq 20$) simply because conspecifics are excluded from the vicinity of one another. These results are robust to variation in threshold distance and survival functional form considered (Figures S1–S4).

A species on the perimeter of our two-dimensional trait space is 0.35–0.50 units from the centre. It therefore appears in Fig. 3d that in models in which species richness is suppressed relative to neutral, enemy-mediated competition effectively excludes most species from the community, excepting those that exploit enemy-free space on the periphery of defence space. The relationship between immigration success and trait distance can be found in Figure S6.

The Papuan Lepidoptera studied by Novotny *et al.* (2010) reveal a strong phylogenetic signal to host use, such that caterpillar similarity declines rapidly as a function of phylogenetic distance between plants and displays a long tail of very low herbivore similarity between distant relatives. In fact, the shape parameter s fitted to these data is 0.0336, or less than the smallest theoretical value we considered (Fig. 1a and b; Table 1). Papuan caterpillars are specialised to a degree that their interaction with host plants closely approximates the strict J-C simulation, supporting 1.95 times as

many species as a neutral model, compared to 2.05 times more species in the case of the strict J-C model (Fig. 4).

The Coleoptera in two Panamanian forests exhibit a similar relationship between host use and plant phylogeny to the herbivores of Papua New Guinea (Fig. 1b and c). As a result, the simulations pertaining to the wet forest of Odegaard *et al.* (2005) maintain an average of 1.90 times as many tree species as a neutral model, and the dry forest 1.94 times more species (Fig. 4). As with the Lepidopteran caterpillars studied by Novotny *et al.* (2010), the Panamanian Coleoptera closely approach the strict J-C model in our simulation. Note also that Figures S1–S4 suggest robustness of these results to variation in R and the form of eqn 5.

The primary difference between the pathogenic fungi studied by Gilbert & Webb (2007) and the insects studied by Novotny *et al.* (2010) and Odegaard *et al.* (2005) was not the shape of the relationship between enemy overlap and plant phylogenetic distance, but rather the per cent overlap at which the relationship reached an asymptote (Fig. 1c), suggesting that distantly related tree species are more likely to share foliar fungal pathogens than insect herbivores. In our simulations, these pathogens maintain an average of 1.40 times more species than extreme generalists, but only 0.67 as many as the strict J-C model (Fig. 4).

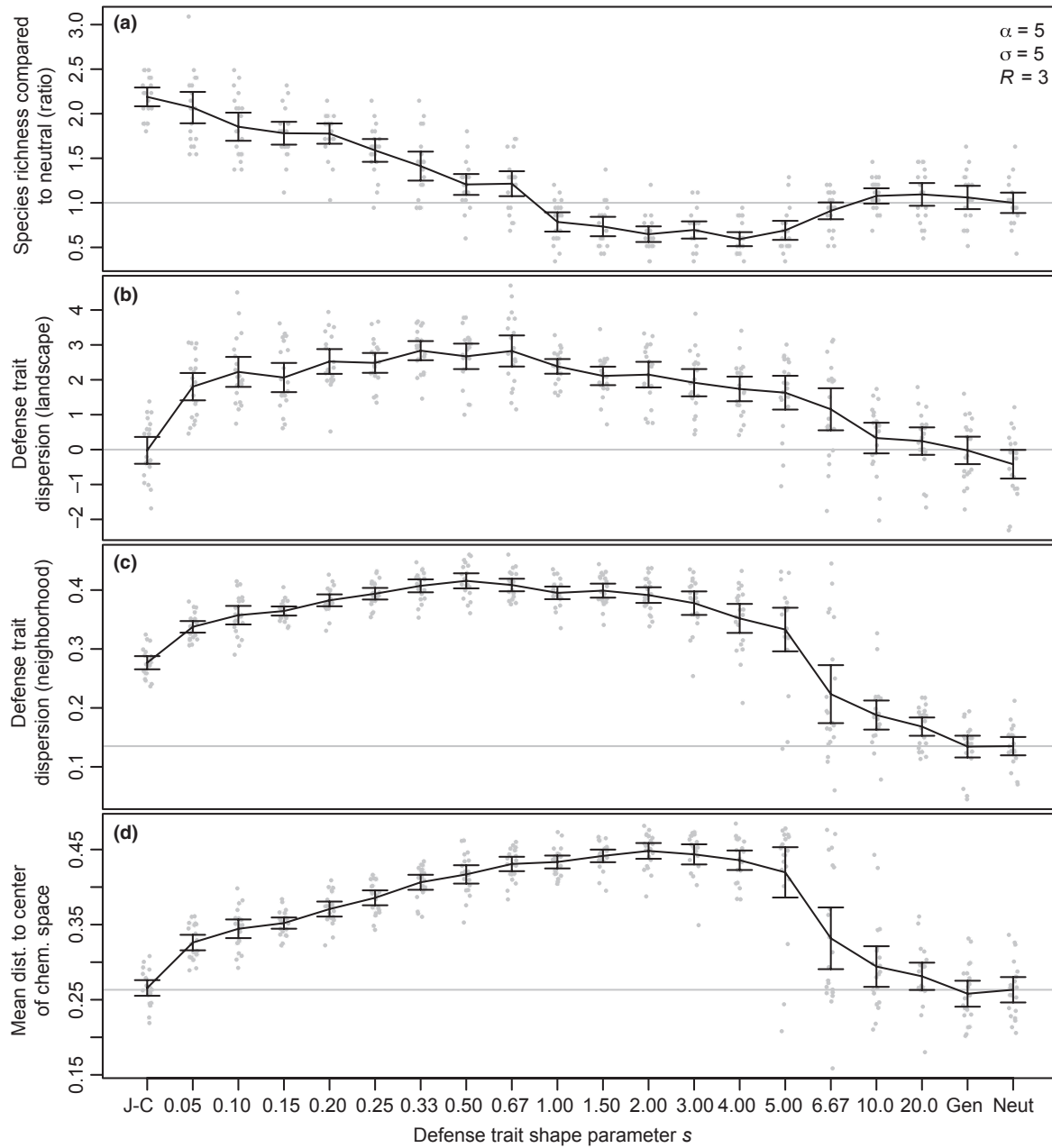


Figure 3 Species richness (a), landscape defence trait structure compared to random species assembly (b), neighbourhood mean trait distance (MTD; (c), and mean distance to the centre of two-dimensional defence trait space (d) as a function of the shape parameter relating enemy overlap to defence trait distance between plant species. MTD was measured between focal individuals and all individuals within 5 m of each focal individual in the simulation landscape. Results shown pertain to an offspring (σ) and enemy (α) dispersal distance of 5 m, an establishment threshold distance (R) of 3 m, and $\beta = 25$. Each point represents the result of one simulation of 400 000 adult deaths. Means and two standard errors of 20 simulations of each model or value of s are indicated.

DISCUSSION

The predictions of Janzen (1970) and Connell (1971) concerning the influence of density-dependent recruitment on the community structure of tropical forests have been largely supported by empirical findings (Wright 2002; Leigh *et al.* 2004; Terborgh 2012). Yet, studies indicate that insects and pathogens are often less specialised than the classical J-C model assumes (Novotny *et al.* 2002; Odegaard *et al.* 2005; Gilbert & Webb 2007), raising the possibility that the diversity and structure of plant communities is also shaped

by generalist enemies (Webb *et al.* 2006; Bagchi *et al.* 2010; Metz *et al.* 2010). Our results suggest that the ability of the J-C mechanism to facilitate the coexistence of plant species is sensitive to the host specificity of plant enemies. However, we also find that strict host specialisation is not a prerequisite for coexistence, as models with narrow host ranges (e.g. $0.05 \leq s \leq 0.67$) support greater species richness than does neutral drift (Fig. 3a). Yet even a shape parameter of $s = 1$, which results in a perfectly proportional decline in enemy similarity with trait distance, fails to enhance plant species richness beyond that maintained in a neutral model.

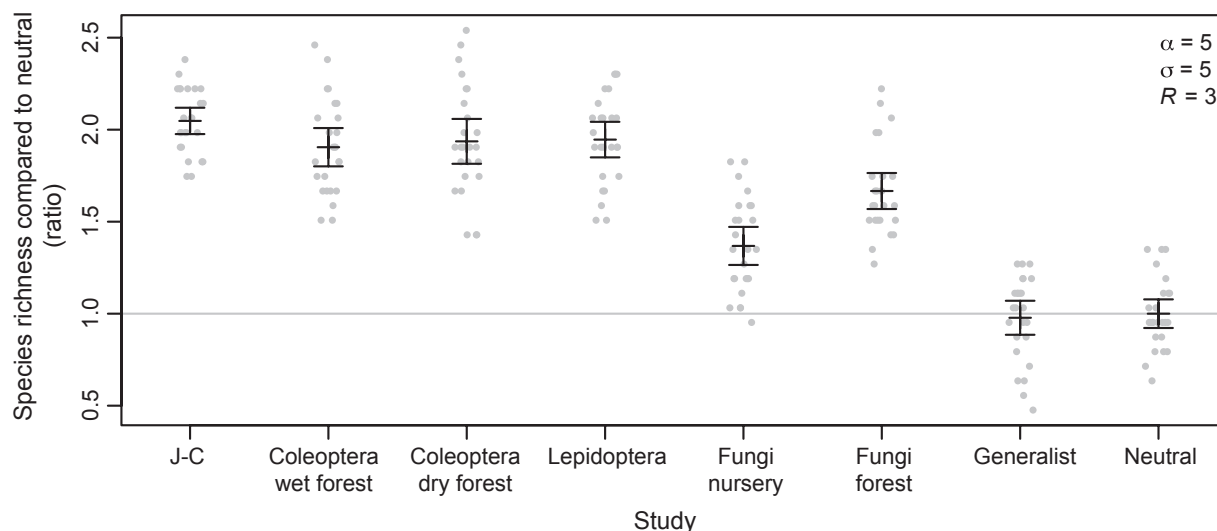


Figure 4 Species richness resulting from simulations parameterised with observed enemy overlap as a function of host-plant phylogenetic distance in three studies. Observed data sets are wet and dry forest Coleoptera in Panama (Odegaard *et al.* 2005), Lepidoptera in Papua New Guinea (Novotny *et al.* 2002) and fungal pathogens studied in a nursery and forest in Panama (Gilbert & Webb 2007). Simulation results from the J-C, Generalist and Neutral models are included for comparison. Results shown pertain to an offspring (σ) and enemy (α) dispersal distance of 5 m and an establishment threshold distance (R) of 3 m. Each point represents the result of one simulation of 400 000 adult deaths. Means and two standard errors of 25 simulations of each model are indicated.

Furthermore, our results suggest that host specificity can determine whether enemy-mediated competition serves to enrich or suppress diversity relative to a neutral model. When $1 \leq s \leq 6.67$, enemy-mediated competition effectively excludes most species from the community, except for those that exploit enemy-free space (Jeffries & Lawton 1984) on the periphery of the two dimensions we use to represent variation in defensive traits. Yet, when s is small – and enemies more specialised – it appears that trait space can be more finely partitioned, and potential immigrants need be only a short trait distance from an abundant resident to successfully invade the community (Figure S6).

On the other hand, the propensity of enemy-mediated competition to increase the trait diversity of plant communities appears quite robust to changes in enemy host specificity. A wide range of models exhibits a substantial signature of non-random community structure with respect to defence, whether considered at the scale of the landscape (Fig. 3b) or of the immediate neighbourhood of each individual plant (Fig. 3c). One important implication is that models that enhance species richness ($0.05 \leq s \leq 0.67$), as well as those that suppress it ($1 \leq s \leq 6.67$), promote trait diversity by favouring dissimilar species within the available dimensions of trait variation. Apparent competition may thus select for novel defensive traits independently of its role as a mechanism of coexistence.

Ehrlich & Raven (1964) postulated that lineage diversification often follows defensive innovation in plants, helping to explain patterns of diversity in plants and their herbivores. Our results suggest that the J-C mechanism is consistent with this idea over a broad range of host specificities. Specifically, trait diversity at neighbourhood and community scales are enhanced over a wide range of host specificity ($0.05 \leq s \leq 6.67$; Fig. 3b and c). Were novel defences to arise through character evolution, rather than immigration, our model suggests that these traits would be quite strongly favoured demographically (Figure S6). We are left to postulate that demographic success associated with enemy release may translate to

increased lineage diversification in taxa in which defences are particularly evolutionarily labile. The absence of phylogenetic signal with respect to defence traits in a number of species-rich genera (Becerra 1997; Agrawal & Fishbein 2006; Kursar *et al.* 2009) and the chemically even spatial structure exhibited by those genera (Becerra 2007; Kursar *et al.* 2009) are consistent with this view.

Are natural enemies specialised enough to facilitate coexistence among plants?

Investigations of phytophagous insects (Novotny *et al.* 2002, 2010) and pathogenic fungi (Gilbert 2005; Gilbert & Webb 2007; Liu *et al.* 2012) in the last decade have generally found less host specialisation than earlier estimates (Lewinsohn & Roslin 2008). There are exceptions to these findings, including studies of insect seed predators, such as beetles in the family Bruchidae (Janzen 1980), and some pathogenic Oomycota (Augspurger 1990). Less specialised enemies have been thought to be unlikely agents of coexistence (Freckleton & Lewis 2006). Nevertheless, the plant diversity maintained by the seemingly generalist insect herbivores examined by Odegaard *et al.* (2005) and Novotny *et al.* (2010) closely approximates that maintained by strictly specialist enemies under conditions in which the strict J-C mechanism is an effective mechanism of coexistence.

Our results suggest that the fungal pathogens studied by Gilbert & Webb (2007) are also sufficiently specialised to foster diversity, but to a lesser extent than in the other two case studies (Fig. 4). However, the strength of diversity maintenance may be understated by fitting s to phylogenetic distance rather than the actual traits that determine host use among pathogenic fungi. Some plant species pairs in their study exhibited no symptoms when cross-infected (Gilbert & Webb 2007). This suggests that the relationship between shared pathogens and plant similarity with respect to relevant defence traits may exhibit a more negative slope than the enemy-phylogeny curve, and asymptote at zero rather than nearly 30%

enemy similarity (Fig. 1b i and ii), and hence maintain greater diversity.

Hanski (1981) has shown that density-responsive predation by generalist enemies can maintain coexistence as long as there is a positive relationship between species abundance and spatial aggregation. Adler & Muller-Landau (2005) found the highest species richness at short enemy and offspring dispersal distances that produced highly clustered adult distributions. Our results confirm Hanski's (1981) conclusion that even generalists can maintain higher species richness than a neutral model when plants are allowed to cluster spatially (Figure S1). While density-responsive generalists may not contribute much to coexistence in closed-canopy forests, this mechanism may enhance species richness in understory, xeric and other spatially aggregated plant communities.

Our model may under-represent the diversity-enhancing effect of shared enemies if such enemies vary in their host preferences, virulence or damage relative to the species that they feed on or infect. Such variation is a key ingredient in the conditions for stable coexistence of species that share enemies, which follow by analogy from resource competition theory (Tilman 1982), and may explain the ability of generalist herbivores to enhance species richness in some instances (Dyer *et al.* 2010). Given n enemies, n plant species may stably coexist if each is unique in the enemy which most limits it, which arises through enemy variation in preferences or effects. Indeed, the deterministic models of Chesson & Kuang (2008) and Bever (2003) show that stable coexistence can result when conspecific negative feedback is more severe than heterospecific feedback due to differences in enemy preferences or effects. Our model accounts for such variation indirectly, by being formulated in terms of the emergent pattern of enemy effects as a function of trait distance, but does not for the empirical data sets, which provide potential rather than actual enemy effects. However, the stochastic, spatial modelling approach we take here permits our model to also account for effects on diversity of increased persistence of species resulting from their differences in their enemy communities, even when those differences do not confer stable coexistence.

On the other hand, the ability of natural enemies to enhance diversity depends on the details of enemy community structure and enemy and seed dispersal. If seed dispersal distances are long relative to enemy dispersal distances, the J-C mechanism maintains fewer plant species than if both enemies and offspring disperse short distances (Adler & Muller-Landau 2005). Furthermore, a negative association between host specificity and enemy virulence or abundance could undermine the diversity-enhancing effect of enemies by allowing dynamics to be dominated by destructive or abundant generalists. Janzen (1988), however, found a positive relationship between host specificity and damage rates in Lepidoptera, and the caterpillars studied by Novotny *et al.* (2010; Fig. 1b) were not dominated by generalists. A greater understanding of the fitness effects and host breadths of plant enemies, and the relationship between the two, would improve models of plant-enemy interactions and coexistence.

CONCLUSIONS

There is broad consensus that the spatially dependent action of specialist enemies described by Janzen and Connell is a widespread and important mechanism that maintains species richness in tropi-

cal forests and other plant communities (Wright 2002; Leigh *et al.* 2004; Terborgh 2012). It remains a challenge to reconcile such patterns with the effects of enemies that associate with a range of often closely related species (Novotny *et al.* 2002; Odegaard *et al.* 2005; Webb *et al.* 2006; Gilbert & Webb 2007; Bagchi *et al.* 2010; Metz *et al.* 2010; but see Janzen 1980). Here, we have shown that the J-C mechanism is indeed sensitive to the host specificity of natural enemies. Within the range of models extending from the J-C model to one in which plant species are indistinguishable in the eyes of enemies, only those that approach the classic J-C model retain the diversity-enhancing effect of the mechanism. Yet, our results also suggest that the case studies of somewhat generalist plant pathogens in Panama and insect herbivores in Panama and Papua New Guinea are sufficiently specialised within their respective plant communities to approach the effectiveness of the classic J-C model at maintaining plant species richness. Future study of the relationship between enemy host use and plant defensive traits in a wider range of systems (both tropical and temperate), and incorporation of that relationship into models like the one we examine here, could provide a more general perspective on the potential influence of enemies on coexistence and spatial organisation in plant communities.

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AUTHORSHIP

BES and AMO designed the research, analysed the data and wrote the manuscript. BES wrote the simulations.

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