letters to nature

Density-dependent mortality and the latitudinal gradient in species diversity

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Ecologists have long postulated that density-dependent mortality maintains high tree diversity in the tropics[1–6]. If species experience greater mortality when abundant, then more rare species can persist[1,2,7–9]. Agents of density-dependent mortality (such as host-specific predators, and pathogens) may be more prevalent or have stronger effects in tropical forests, because they are not limited by climatic factors[1–5]. If so, decreasing density-dependent mortality with increasing latitude could partially explain the observed latitudinal gradient in tree diversity[4–6]. This hypothesis has never been tested with latitudinal data. Here we show that several temperate tree species experience density-dependent mortality between seed dispersal and seedling establishment. The proportion of species affected is equivalent to that in tropical forests[6,10–16], failing to support the hypothesis that this mechanism is more prevalent at tropical latitudes. We further show that density-dependent mortality is misinterpreted in previous studies. Our results and evidence from other studies suggest that density-dependent mortality is important in many forests. Thus, unless the strength of density-dependent mortality varies with latitude, this mechanism is not likely to explain the high diversity of tropical forests.

We used a demographic study of temperate forest species to determine whether survival probabilities at early life-history transitions decrease when seeds or seedlings are at high densities or close to adults of the same species (conspecific). We quantified seed dispersal, seed bank densities, seedling emergence and seedling survival at 100 microsites distributed across five temperate forest stands over 3 years. We then determined whether transition probabilities across early life-history stages were lower at high conspecific seed and seedling densities or close to conspecific trees, a phenomenon said to promote species diversity, called the 'Janzen–Connell' effect[1,2]. We tested transitions from dispersed seed to seed bank (incorporation), seed bank to germinated seedling (germination), germinated seedling to established seedling (establishment), and first-year seedling to second-year seedling (survival). We also determined whether effects of conspecific density (seeds, seedlings) or distance (proximity to conspecific trees) on mortality are greater than are effects of other species, a requirement if density-dependent mortality is to promote species diversity[1,9].

Six of the seven temperate forest taxa we tested (*Acer pennsylvanicum*, *Acer rubrum*, *Betula* spp., *Fraxinus americana*, *Liriodendron tulipifera* and *Quercus rubra*) experience density-dependent mortality at one or more life-history transitions, with greater effects of conspecific seed and seedling density or conspecific adult proximity on mortality than of heterospecific (different species) (Table 1). Survival of seeds in the soil (three of three species with long-term seed banks) and seedling emergence (five of seven species) was reduced at high conspecific seed densities, close to conspecific trees, or both. For example, the proportion of *Acer rubrum* seeds germinating in 1×1 m plots is depressed at high seed rain densities (Table 1, Fig. 1). Because the negative effects of conspecifics are much greater than those of heterospecifics (Table 1), they are likely to result from host-specific seed predators or pathogens[17–21] rather than resource competition with other seedlings or adults. Regardless of what causes seedling mortality, our analyses identified the kind of density-dependent mortality that promotes species diversity by disproportionately affecting species when they are abundant[10,15].

The high numbers of tree species experiencing density-depen-

Table 1 Parameter estimates and probabilities from best-fitting models

Species Transition	Intercept	Conspecific effects		Heterospecific effects		Density-dependent mortality		Conspecific > heterospecific effects	
		Juveniles	Adults	Juveniles	Adults				
	v_j	d_j	a_j	d	a	$(d_j = 0)$	$(a_j = 0)$	$(d_j = d)$	$(a_j = a)$
Acer pennsylvanicum									
Germination	1.54×10^{-1}	8.27×10^{-2}	–	1.26×10^{-5}	–	<0.001	NS	<0.001	NS
Establishment	2.24×10^{-1}	–	-5.91×10^{0}	–	-8.71×10^{-1}	NS	NS	NS	NS
Survival	7.33×10^{-1}	6.00×10^{-2}	-5.17×10^{0}	6.00×10^{-2}	-3.04×10^{-1}	0.028	0.022	NS	0.027
Acer rubrum									
Incorporation	1.29×10^{-1}	4.57×10^{-2}	–	3.71×10^{-4}	–	<0.001	NS	<0.001	NS
Germination	3.07×10^{-1}	5.15×10^{-2}	5.36×10^{-1}	2.77×10^{-5}	5.36×10^{-1}	<0.001	0.020	<0.001	NS
Establishment	1.91×10^{-1}	-1.38×10^{-2}	–	-1.38×10^{-1}	–	<0.001	NS	NS	NS
Survival	4.49×10^{-1}	-1.10×10^{-2}	–	1.18×10^{-2}	–	<0.001	NS	<0.001	NS
Betula spp.									
Incorporation	2.97×10^{-2}	2.92×10^{-4}	1.14×10^{1}	-2.90×10^{-3}	-8.26×10^{-1}	<0.001	<0.001	<0.001	<0.001
Germination	1.79×10^{-3}	3.38×10^{-3}	–	-1.38×10^{-3}	–	<0.001	NS	0.002	NS
Establishment	9.89×10^{-1}	–	8.76×10^{0}	–	8.76×10^{0}	NS	0.007	NS	NS
Survival	1.03×10^{-4}	4.88×10^{-2}	-4.06×10^{1}	4.88×10^{-2}	-4.06×10^{1}	0.004	0.029	NS	NS
Fraxinus americana									
Germination	1.760×10^{-1}	2.61×10^{-1}	–	5.23×10^{-4}	–	0.008	NS	0.009	NS
Establishment	3.79×10^{-1}	–	–	–	–	NS	NS	NS	NS
Liriodendron tulipifera									
Incorporation	9.99×10^{-2}	1.26×10^{-2}	-5.97×10^{0}	5.77×10^{-4}	-1.01×10^{-1}	<0.001	0.002	<0.001	0.003
Germination	2.66×10^{-3}	6.89×10^{-3}	-6.49×10^{0}	6.89×10^{-3}	4.51×10^{0}	0.039	NS	NS	0.008
Establishment	3.99×10^{-1}	2.53×10^{-2}	–	2.53×10^{-2}	–	0.007	NS	NS	NS
Quercus rubra									
Germination	1.89×10^{-2}	9.16×10^{-3}	3.84×10^{0}	9.16×10^{-3}	-5.54×10^{0}	<0.001	NS	NS	0.008
Establishment	7.64×10^{-1}	–	–	–	–	NS	NS	NS	NS
Survival	4.29×10^{-1}	–	–	–	–	NS	NS	NS	NS
Vitis spp.									
Germination	4.70×10^{-4}	–	–	–	–	NS	NS	NS	NS

A dash indicates that the parameter not significantly different from 0, as determined from likelihood ratio tests. NS, $P > 0.05$, not significant.

dent mortality in the tropics is sometimes hypothesized to explain the latitudinal gradient in species diversity[4–6]. Our results showing high levels of density-dependent mortality in temperate forests (and studies in Texas[22] and South Carolina[23]) led us to examine the relationship between latitude and the proportion of tree species experiencing density-dependent mortality from ten studies in eight forest communities (two in Australia[10,14], two in Indonesia[12,15,16], one in Panama[6,11,13,16], and three in southeastern USA—Texas[22], South Carolina[23] and our site in North Carolina). We found no

Figure 1 The observed (**a**) and predicted (**b**) relationship between conspecific seed density and seed germination for *Acer rubrum*. **a**, Each circle represents a paired seed trap and seedling quadrat in 1 of 3 years. **b**, The best-fit relationship between germination and density of conspecific seeds (see Methods); dashed lines are 95% bootstrapped confidence intervals. Likelihood ratio tests indicate that germination decreases at high conspecific densities.

Figure 2 The proportion of tree taxa experiencing density-dependent mortality at different latitudes. Each bar corresponds to an analysis testing a community of forest trees for the presence of density-dependent mortality (our analyses and previous studies[6,10–16,22,23]). The proportion of the forest community experiencing density-dependent mortality does not increase at tropical latitudes.

evidence that the proportion of species experiencing density-dependent mortality is correlated with latitude (Spearman's rank correlation = 0.028, $P > 0.9$). Thus, although the magnitude of density-dependent mortality (that is, strength of effects) could be higher in tropical forests (we have no evidence that it is), the prevalence of density-dependent mortality (that is, number of species affected) is not associated with latitude.

The role of density dependence in promoting forest tree diversity has been extensively debated[8,11,12,24–29]. Empirical studies have not resolved this question, because the number of species interpreted as experiencing density-dependent mortality varies among studies, even within the same forest (for example, studies at Pasoh[12,13] and Barro Cobrado Island[6,11,13,16]; Fig. 2). We re-analysed our data using assumptions employed by studies reporting variable levels of density-dependent mortality in forests[6,11–14,16] and found that the different results may reflect methods of analysis rather than underlying differences in the prevalence of density-dependent mortality (see Methods and Fig. 3).

Using methods employed in previous studies, we might have concluded that all species at all life-history stages experience density-dependent mortality (Fig. 3e) or that no species experience density-dependent mortality at any life-history stage (Fig. 3d). Density-dependent mortality at early life-history stages may be underestimated if only effects of adult trees[11,12] are quantified, that is, if negative effects of juvenile conspecifics are ignored (compare Fig. 3a, b). In contrast, failing to distinguish between con- and heterospecific effects[6,12,29] can lead to overestimation of density-dependent mortality (compare Fig. 3a, c), because effects must be species-specific to foster coexistence of species[1,9]. Owing to dispersal, initial seed densities are highest around parent trees, and often remain so in spite of high mortality at high densities of seeds or seedlings or close to parent trees. Analyses that ignore dispersal by testing whether densities of recruits increase with distance from conspecific trees[12,14] can therefore underestimate density-dependent mortality (compare Fig. 3a, d). Statistics used to indicate density-dependent mortality in one study[6] overestimate the prevalence of this mechanism relative to other methods (compare Fig. 3a–d with e). Finally, more species experience density-dependent mortality at the earliest life-history stages[2], regardless of methodology (Fig. 3). Studies performed on later life-history transitions[11–13,16] thus underestimate the number of taxa affected by density-dependent mortality. Overall, the prevalence of density-dependent mortality has probably been underestimated in forests, because density-dependent mortality is most prevalent at seed and seedling stages (Fig. 3), and most studies reporting low density-dependent mortality are performed at later life-history stages[11–13,16].

High density-dependent mortality in temperate forests (Table 1) and the lack of a latitudinal gradient in density-dependent effects (Fig. 2) do not support the view that density-dependent mortality is responsible for the latitudinal gradient in species diversity. We find that density-dependent mortality is as common in temperate forests as in tropical forests (as do other studies[21–23]). Confusion has resulted from analyses that ignore dispersal or are applied at later life-history stages, both of which underestimate density-dependent mortality (Fig. 3). The ubiquity of density-dependent mortality may mean this mechanism contributes to tree diversity in forests worldwide, if effects at early life-history stages promote diversity at later life-history stages (with one exception[6], rarely tested). Absence of evidence for latitudinal trends in density-dependent mortality implies that other mechanisms are responsible for high diversity in the tropics. □
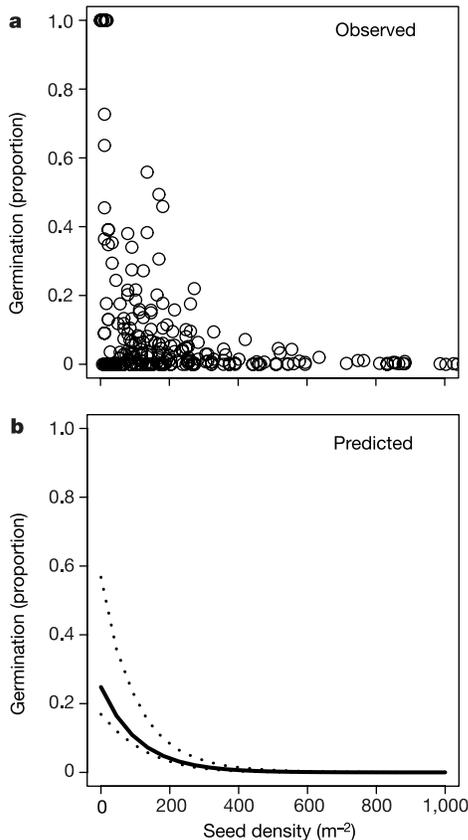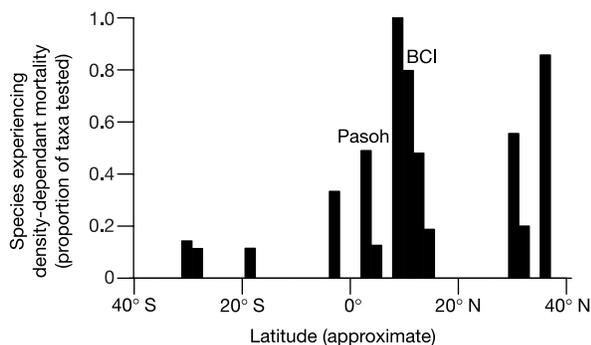
Methods

Study site and experimental design

Studies were performed in secondary temperate deciduous forests at the Coweeta Hydrologic Laboratory (western North Carolina). We identified and mapped all trees more than 2 m tall in five 80 × 80-m permanent vegetation plots[30]. Twenty seed traps were

located within each plot. Seed traps were mesh-lined baskets ($0.1764\,m^2$) suspended 1 m above the ground and covered with wire mesh to deter seed predation[30]. Traps were emptied four times annually, and seeds identified and counted[30]. Soil cores ($0.0062\,m^2$, 0.05 m deep) adjacent to each trap were removed in autumn 1996, 1997 and 1998. In Duke University's greenhouses, soil was spread over sterile potting soil, and seedlings (each representing a viable seed) were counted and identified as they emerged. In the field, seedlings were identified and tagged in during summer 1997, 1998 and 1999 in quadrats ($1.0\,m^2$) adjacent to each seed trap.

For seven species having sufficient densities to perform analyses, we tested whether four life-history transitions (incorporation, germination, establishment and survival) are affected by conspecific juvenile densities or adult proximity. Analyses were performed on data from 3 years, except for seed incorporation into the soil, where data were averaged across years (because seeds survive more than 1 year in the soil). Results were consistent when data were analysed as averages across years, or separately by plot and by year.
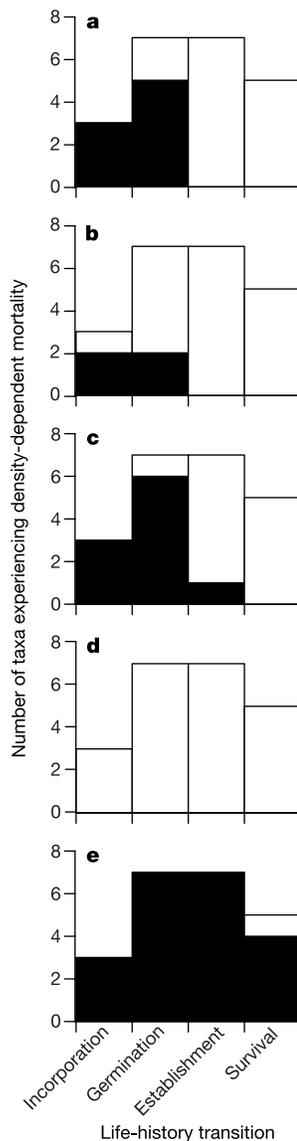

Figure 3 Five analyses used to test for density-dependent mortality are applied to seed bank incorporation, germination, establishment and over-winter survival. **a**, Our analyses (equations 1 and 2). **b**, Tests that ignore density-dependent mortality due to high juvenile densities. **c**, Tests that do not differentiate conspecific density-dependent mortality from heterospecific density-dependent mortality. **d**, Tests that ignore effects of dispersal on seed and seedling distributions (equation (3)). **e**, Regression of logged data to test whether survival decreases at high densities (equations (4), (5) and (6)). Both analyses employed and life-history transitions tested strongly influence conclusions about the prevalence of density-dependent mortality.

Estimation and testing

For transitions from life-history stage $k-1$ to k for species j, we used the binomial likelihood to estimate transition probabilities (P_{ijk}) and to test for density-dependent mortality in T quadrats:

$$L_{jk} = \prod_{i=1}^{T} \mathrm{Bin}(n_{ijk}|n_{ij(k-1)}, P_{ijk}(v_{jk}, d_{jk}, d_k, a_{jk}, a_k)) \quad (1)$$

The probability of survival of species j at quadrat i,

$$P_{ijk} = v_{jk}\exp\left[-d_{jk}n_{ij(k-1)} - d_k\sum_{m\neq j}n_{im(k-1)} - a_{jk}\sum{}^{b_j}/x_{ij} - a_k\sum_{m\neq j}{}^{b_m}/x_{im}\right] \quad (2)$$

depends on conspecific juvenile densities at quadrat i ($n_{ij(k-1)}$) and juvenile densities of all other species ($n_{im(k-1)}$). Density dependence means that fitted parameters d_{jk} and d_k are greater than zero. If transition probabilities are decreased close to surrounding adult trees (basal area b_j at distance x_{ij} metres), fitted parameters a_{jk} and a_k are greater than zero. A more traditional analysis of distance-dependent mortality[2] did not change our results, and led to poorer model fits (as determined by Akaike's information criterion). The transition probability tends to v_{jk} at low juvenile densities, far from adult trees, or when there are no effects of juveniles or adults.

We used likelihood ratio tests to determine whether conspecific juveniles have stronger effects on transition probabilities than other species ($d_{jk} > d_k$), or whether mortality is more strongly affected by conspecific trees than by heterospecific trees ($a_{jk} > a_k$). In the few cases where seed bank or seedling densities within quadrats were greater than incoming seed densities in neighbouring seed traps, we assumed seed densities were equivalent to seed bank or seedling densities for these quadrats. We repeated analyses excluding those sampling sites, and found consistent results.

Comparisons with other studies

To determine whether methodology accounts for differences among studies in the proportion of taxa affected by density-dependent mortality, we compared the number of taxa experiencing density-dependent mortality using likelihood ratio tests and equations 1 and 2 (Fig. 3a) with those obtained using four approaches in previous studies (Fig. 3b–e).

The first analysis assumes that only adult trees cause density-dependent mortality. We re-analysed our data in a comparable fashion by assuming no effects of juveniles on P_{ijk}, by setting d_{jk} and d_k in equation 2 to zero (Fig. 3b). The second analysis assumes that there are no heterospecific effects (either adult or juvenile) on early life-history transitions. For this analysis, we set both d_k and a_k in equation 2 to zero (Fig. 3c). The third method assumes that mortality close to conspecific trees depresses recruitment, and that seedling densities increase with distance from trees. We examined this assumption by testing whether seed, seed bank or seedling densities (n_{ijk}) were positively correlated with the distance of each quadrat (x_{ij}) to its nearest conspecific tree (fitted parameter $b_{jk} > 0$):

$$n_{ijk} = a_{jk} + b_{jk}x_{ij} \quad (3)$$

using a negative binomial likelihood (Fig. 3d). This test is analogous to that made in several studies[12,14] of density-dependent mortality, although we used an error distribution more appropriate for count data.

The fourth method tests whether juvenile densities (n_{ijk}) saturate at high inputs ($n_{ij(k-1)}$):

$$n_{ijk} = a \times (n_{ij(k-1)})^b \quad (4)$$

Fitted parameters are b and c. We fitted this relationship in a manner similar to that in a recent study[6]—with a linear regression using values logged after adding one:

$$\ln(n_{ijk}+1) = \ln b + c\ln(n_{ij(k-1)}+1) + \varepsilon_{ij} \quad (5)$$

with normally (N) distributed error:

$$\varepsilon_{ij} \sim N(0,\sigma^2) \quad (6)$$

With this analysis, density-dependent mortality is indicated by a slope parameter, c, being less than one (Fig. 3e). The addition of a constant to juvenile densities n_{ijk} (in this case, one) before log transformation underestimates the slope parameter (c), potentially overestimating density-dependent mortality.

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Competing interests statement

The authors declare that they have no competing financial interests

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Geographic structure and dynamics of coevolutionary selection

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Coevolution of species is one of the major processes organizing the Earth's biodiversity. Recent coevolutionary theory has indicated that the geographic structure of species has the potential to impose powerful and continuing effects on coevolutionary dynamics, if that structure creates selection mosaics and coevolutionary hotspots across landscapes[1–7]. Here we confirm that current coevolutionary selection in interspecific interactions can be highly divergent across both narrow and broad geographic scales, thereby fuelling continuing coevolution of taxa. Study of a widespread plant–insect interaction across a broad range of habitats for several years showed that an insect functioning both as a pollinator and a floral parasite can be strongly

mutualistic in some habitats but commensal or antagonistic in neighbouring habitats. The results for one of the habitats span seven years, demonstrating that the local structure of coevolutionary selection can remain stable across multiple generations. Conservation of the evolutionary processes maintaining long-term biological diversity may require preservation of the conditions that allow a long-term shifting geographic mosaic of coevolutionary hotspots and coldspots.

Although some coevolving interactions show little spatial variation in outcome[8], evidence for pronounced geographic differences in interspecific interactions has now been found in a diverse array of interactions, including those between parasites and hosts, predators and prey, competitors, and mutualists[9–18]. The geographic mosaic theory of coevolution indicates that these geographic differences are an inherent part of the coevolutionary process, driven by variation between habitats in the trajectories of natural selection (selection mosaics), the occurrence of reciprocal selection in only some communities (coevolutionary hotspots), and a constantly changing
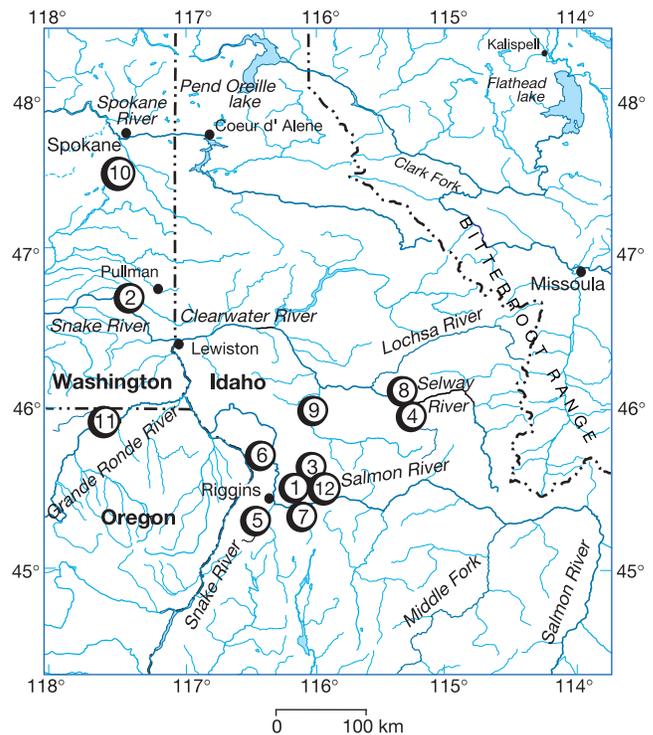

Figure 1 Distribution of study sites for analysis of coevolutionary hotspots in the interaction between the plant *Lithophragma parviflorum* and the moth *Greya politella*. Locations: 1, Berg = Berg Mountain, Salmon River, Idaho (ponderosa pine woodland); 2, Granite = Granite Point, Snake River, Washington (canyon bottom meadow steppe); 3, Keating = Keating Ridge, above Salmon River, Idaho (ridgetop grassland with ponderosa pine); 4, Meadow = Meadow Creek near confluence with Selway River, Idaho (streamside meadow amid grand fir and western red cedar); 5, Rapid = Rapid River above confluence with Little Salmon River, Idaho (streamside narrow canyon amid Douglas fir and Pacific yew); 6, Saddle = near Pittsburg Saddle above Snake River, Idaho (high-elevation open ridge top with scattered ponderosa pines); 7, Salmon = along Salmon River east of Riggins, Idaho (north-facing steppe); 8, Selway = lower Selway River, Idaho (openings in habitat dominated by western red cedar, Douglas fir and ponderosa pine); 9, South Fork = South Fork of Clearwater River, Idaho (open ponderosa pine savanna); 10, Turnbull = Turnbull National Wildlife Refuge, Washington (ponderosa pine woodland on glacial polygonal soil); 11, Wenaha = Wenaha River, Idaho (south-facing steppe with thick shrub cover); 12, Wind = Gospel Hump Wilderness along Salmon River, Idaho (dry, south-facing steppe).

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