REVIEW AND SYNTHESIS

Trait-based tests of coexistence mechanisms

Peter B. Adler,[1]* Alex Fajardo,[2]
Andrew R. Kleinhesselink[1] and
Nathan J. B. Kraft[3]

Abstract

Recent functional trait studies have shown that trait differences may favour certain species (environmental filtering) while simultaneously preventing competitive exclusion (niche partitioning). However, phenomenological trait-dispersion analyses do not identify the mechanisms that generate niche partitioning, preventing trait-based prediction of future changes in biodiversity. We argue that such predictions require linking functional traits with recognised coexistence mechanisms involving spatial or temporal environmental heterogeneity, resource partitioning and natural enemies. We first demonstrate the limitations of phenomenological approaches using simulations, and then (1) propose trait-based tests of coexistence, (2) generate hypotheses about which plant functional traits are likely to interact with particular mechanisms and (3) review the literature for evidence for these hypotheses. Theory and data suggest that all four classes of coexistence mechanisms could act on functional trait variation, but some mechanisms will be stronger and more widespread than others. The highest priority for future research is studies of interactions between environmental heterogeneity and trait variation that measure environmental variables at within-community scales and quantify species' responses to the environment in the absence of competition. Evidence that similar trait-based coexistence mechanisms operate in many ecosystems would simplify biodiversity forecasting and represent a rare victory for generality over contingency in community ecology.

INTRODUCTION

Plant ecologists are investing tremendous effort in understanding communities through the lens of functional traits (Grime 1977; Weiher & Keddy 1995; McGill *et al.* 2006; Westoby & Wright 2006; Shipley 2010). By capturing essential aspects of species' ecophysiology, morphology and life-history strategy, functional traits offer a mechanistic link between fundamental biological processes and community dynamics (McGill *et al.* 2006; Westoby & Wright 2006). Furthermore, because traits offer a common, taxon-independent currency for species comparisons, trait-based approaches have the potential to reveal general, synthetic and predictive relationships that studies of idiosyncratic, species-specific responses have failed to identify. One of the most ambitious goals of the trait-based programme is to understand how traits mediate community assembly and coexistence to predict the effects of global change on biodiversity (e.g. Suding *et al.* 2005). Our objective is to direct future research towards approaches with the greatest potential for achieving this goal.

Current trait-based approaches in community ecology focus on analyses of trait dispersion patterns to detect environmental filtering and niche partitioning. Evidence for environmental filtering comes from correlations between environmental gradients and community-weighted trait values (Kraft *et al.* 2008; Cornwell & Ackerly 2009;

Swenson & Enquist 2009; Kraft & Ackerly 2010; Shipley 2010; Katabuchi *et al.* 2012) and from studies showing that trait differences generate competitive hierarchies (Freckleton & Watkinson 2001; Kunstler *et al.* 2012). Evidence that traits play a role in maintaining species diversity through niche partitioning comes from the great variation in trait values found within most communities (e.g. Westoby *et al.* 2002) and from studies showing that trait values of co-occurring species are over-dispersed relative to expectations from null models (Stubbs & Wilson 2004; Kraft *et al.* 2008; Paine *et al.* 2011). The rationale is that species with different traits may have different resource or habitat requirements and will compete less intensely than species with similar traits. While much of this recent work has focused on plant communities, there is a long history of exploring phenotypic trait dispersion in animal assemblages (Ricklefs & Travis 1980) and non-random dispersion patterns within communities have been documented in a wide range of phyla (e.g. Rabosky *et al.* 2007; Ingram & Shurin 2009; Gómez *et al.* 2010). These studies provide compelling evidence that trait variation influences community assembly and coexistence.

Existing trait-based approaches represent important advances, but ultimately they cannot provide the mechanistic understanding necessary to predict the effect of local and global change on species diversity. Trait-based prediction of how nitrogen (N) deposition or climate change may impact species diversity requires information

[1]*Department of Wildland Resources and the Ecology Center, Utah State University, Logan, UT, 84322, USA*
[2]*Centro de Investigación en Ecosistemas de la Patagonia (CIEP) Conicyt–Regional R10C1003, Universidad Austral de Chile, Ignacio Serrano 509, Coyhaique, Chile*

[3]*Department of Biology, University of Maryland, College Park, MD, 20742, USA*
Correspondence: E-mail: peter.adler@usu.edu

about which coexistence mechanisms are most important in a given community and how they act on functional trait variation. For example, N deposition could cause dramatic decreases in diversity if resource partitioning is the key coexistence mechanism, but might have a minimal effect if coexistence is mediated primarily by fine-scale spatial variation in soil moisture (Silvertown *et al.* 1999). Models based on environmental filtering (Shipley 2010; Shipley *et al.* 2011) successfully predict variation in species relative abundances along environmental gradients. However, these models are not designed to address our goal of understanding and predicting the impact of environmental change on species diversity. Trait dispersion analyses do focus on explaining the maintenance of diversity within local communities and can successfully identify traits involved in niche partitioning, but do not provide any predictive capability. Even the strongest phenomenological evidence that functional trait variation promotes coexistence (Uriarte *et al.* 2010) or increases species richness (Ben-Hur *et al.* 2012) will not help us to predict the effect of a particular environmental change, such as N deposition, on diversity. To use functional traits to understand and predict the impact of perturbations on biodiversity, we need to know *how* trait differences promote coexistence.

Achieving the ambitious goals of trait-based community ecology requires a shift from phenomenological studies of trait dispersion patterns towards trait-based tests of recognised coexistence mechanisms. Our first objective is to demonstrate why trait dispersion studies ultimately cannot provide the mechanistic understanding necessary to predict the effect of local and global change on species diversity. We use a simple simulation model to illustrate the limitations of trait dispersion analyses and the benefits of a more mechanistic approach. Our second objective is to provide researchers with a road map for linking functional traits with well-known mechanisms of species coexistence involving spatial heterogeneity, temporal heterogeneity, resource partitioning and natural enemies (Chesson 2000). For each of these mechanisms, we (1) modify existing tests, which are designed to handle data aggregated by species, to accommodate data that represent continuous variation in functional traits, (2) develop hypotheses about which particular functional traits have the most potential to promote coexistence via the mechanism in question and (3) review the literature for relevant evidence or conspicuous information gaps. While the coexistence tests we propose could be applied to any trait and any kind of organism, most trait dispersion analyses have focused on plant communities where the problem of coexistence is particularly vexing, since all plants compete for a limited number of resources. Therefore, our literature review focuses on the most widely measured plant functional traits: seed size, which influences how many propagules a plant can produce and the resources invested in each individual propagule, wood density, which mediates a trade-off between rapid vertical growth and resistance to damage, and traits related to the leaf economics spectrum including specific leaf area (SLA), the ratio of leaf area to dry weight, leaf N concentration and leaf life span.

LIMITATIONS OF THE TRAIT DISPERSION APPROACH

To illustrate how trait variation can promote coexistence, and to demonstrate the limitations of trait dispersion analyses, we built a simulation model in which coexistence depends entirely on the interaction between fine-scale variation in resource availability and variation in seed size (Box 1). We assumed that large seeds can tol-erate low resource availability but have lower fecundity than smaller seeded species (Muller-Landau 2010). As a result of this tolerance-fecundity trade-off, mean seed size decreases with mean resource availability in the local community, while local species richness increases with variation in resource availability within the community (Fig. 1). Running the simulated output through a trait dispersion analysis shows evidence for both environmental filtering (clustering of seed sizes across communities) and niche partitioning (even spacing of seed sizes within communities). While these trait dispersion patterns are typical of many empirical studies, they limit understanding in three important ways.

First, trait dispersion tests have low power to detect niche partitioning (Kraft & Ackerly 2010). In our simulations, variation in seed size is the only way that species can partition this virtual environment, yet we found significant evidence for over-dispersed spacing of seed sizes in only 75% of the high richness communities and 33% of the low richness communities (Box 1, Fig. 1d). The low power of trait spacing tests is compounded by the problem that a lack of evidence for even spacing cannot be interpreted as evidence against a role of competition in community assembly (Mayfield & Levine 2010).

Second, patterns typically interpreted as environmental filtering and niche partitioning may be generated by the same process. The common interpretation is that species interactions play no role in the abiotic environmental filtering process, while abiotic factors play no role in the competitively driven niche partitioning process. However, the dichotomy between environmental filtering and niche partitioning can arise from an arbitrary decision about the spatial scale of analysis, not from distinct biological processes. Our simulations show that it is wrong to characterise the between-community trend in mean seed size as solely environmental filtering because it reflects, in part, competitive exclusion. The largest seeded species could occur in any cell in any of our simulated communities, but they are excluded by smaller seeded competitors that can tolerate the same cells but have higher fecundity. Conversely, it would be incorrect to characterise the within-community pattern as a purely biotic outcome of competitive exclusion because environmental heterogeneity is what makes niche partitioning at this scale possible. In fact, viewed at a finer, within-community spatial scale, niche partitioning is simply environmental filtering, with species sorted into different microsites based on their seed sizes (Fig. 1c). Our simulation, in which spatial heterogeneity generates coexistence, makes this especially clear, but the general point would hold even if another mechanism, such as seed size-specific natural enemies, maintained within-community diversity.

Third, phenomenological studies of trait variation patterns cannot answer two of the most important basic and applied questions about diversity: Why is species richness higher in some communities than in others? How will future perturbations alter species richness? These questions fall outside the scope of trait pattern studies because observed levels of species richness are taken as the starting point for the analysis. Specifically, since most trait spacing measures are trivially correlated with species richness, the analyses are conditioned on observed richness. Unfortunately, simply knowing that seed size variation may promote coexistence given the observed richness (which the trait pattern analysis can tell us) does not help us identify factors that would increase or decrease richness. In contrast, a mechanistic approach that identifies how traits interact with the environment can explain differences in richness among sites and offers

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Box 1 A simulation case study

To demonstrate how trait variation can generate coexistence, we simulated a simple, theoretical model. We then analysed trait dispersion patterns in the simulation output to illustrate the limitations of this phenomenological approach. Our model assumes that variation among species in seed size generates a strict trade-off between fecundity and tolerance of low resource availability. In the presence of spatial variation in resources, this trade-off can promote coexistence (Muller-Landau 2010). The simulation proceeds in four steps (R scripts provided in Supplementary Information):

(1) Create a species pool. Assign each hypothetical species a seed size, with seed sizes increasing from 1 to 4400 in intervals of 1. Resource requirements and fecundity are decreasing linear functions of seed size (large seeds can tolerate lower resource availability but produce fewer seeds).

(2) Create the local environment. Each community consists of 88000 cells, with each cell supporting one individual plant. Each cell is assigned a resource availability value, drawn from a normal distribution with mean, μ, and standard deviation, σ.

(3) Initialise the community, filling each cell with one plant based on an evenly weighted lottery among all species that can tolerate the resource availability of the cell.

(4) Disturb and colonise cells. At each time step, each cell is disturbed with probability 0.1. Recolonisation of each disturbed cell is a *weighted* lottery among the species that can tolerate the cell, with the weights determined by the relative seed production of each species across all cells.

As mean resource availability, μ, increases, community-weighted mean seed size decreases (Fig. 1a). Species richness depends on spatial heterogeneity in resources, σ (Fig. 2a). When $\sigma = 0$, only one species persists, but as σ increases richness increases as well. Thus, variation in seed size is not sufficient for coexistence; coexistence results from the interaction between seed size and spatial heterogeneity within the community. Within communities, a strong relationship emerges between seed size and local resource availability, with large-seeded species occurring on the low resource microsites, and small-seeded species occurring on the high resource microsites (Fig. 3a). This within-community relationship between seed size and microsite resource availability mirrors the between-community relationship between mean seed size and mean resource availability.

We next analysed the trait dispersion patterns (Kraft & Ackerly 2010) of the communities in which richness was greater than one. Evidence for environmental filtering was clear: In every community, the mean, range and variance in seed size was significantly different from the null expectation. We also found evidence for high trait dispersion: The standard deviation of nearest neighbour distances among co-occurring species, corrected for total high trait range, was lower than the (non-parametric) null expectation in 22 of the 30 high-heterogeneity communities and 9 of the 30 intermediate heterogeneity communities (Fig. 1d). The interpretation of these results is that variation in seed size plays a role in maintaining diversity. In the main text (*Limitations of the trait dispersion approach*), we explain why this conclusion represents just a starting point for research on traits and coexistence.

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predictions about how perturbations will affect diversity. If the simulation results illustrated in Fig. 1b and c had come from a natural community, the lesson would be clear: factors which reduce local spatial heterogeneity in resource availability will decrease richness.

Although our simulation involves interspecific variation in traits, it is also relevant to research on intraspecific trait variation, which recent studies have shown may influence community-level processes (Violle *et al.* 2012). When intraspecific studies focus on patterns of trait dispersion to make inferences about competition (Jung *et al.* 2010; Violle *et al.* 2012), they are limited by the same constraints as their interspecific analogues. Testing mechanistic hypotheses should be just as important for coexistence mechanisms based on intraspecific variation.

To help empiricists move from trait pattern analyses to tests of coexistence mechanisms, we need to identify the additional data that will be most important to collect. In our simulation of the tolerance-fecundity trade-off, the key to understanding coexistence is data on resource availability at the within-community scale. As our review of the empirical literature will demonstrate, this information is almost never reported. In fact, the absence of this data is what created the need for trait dispersion tests, which offer a phenomenological proxy for the underlying processes of interest. Of course, data on spatial environmental heterogeneity are not the only relevant type. Depending on the coexistence mechanism, data on spe-

cies responses to temporal environmental fluctuations, resource limitation, or natural enemies may also be important. Our objective is to narrow the list of candidate covariates by identifying the most promising mechanisms for each trait.

INCORPORATING FUNCTIONAL TRAITS IN COEXISTENCE THEORY

Trait dispersion analyses show that a difference in a functional trait can give one species an advantage over another through environmental filtering, while also preventing competitive exclusion through niche partitioning. But how can both processes operate simultaneously? How can a difference in, say, SLA between two species give one of those species a competitive advantage but also prevent competitive exclusion? This paradox can be illustrated with the coexistence criteria for a two-species Lotka-Volterra competition model,

$$\frac{1}{\alpha_{21}} > \frac{K_1}{K_2} > \frac{\alpha_{12}}{1}$$

where the K's are the carrying capacities and α_{ij} is the per capita effect of species j on species i (intraspecific effects, the α_{ii}'s, are set to 1). Incorporating the competitive advantages that drive environment filtering is straightforward: each species' carrying capacity, K, could be a function of the distance between some optimal trait
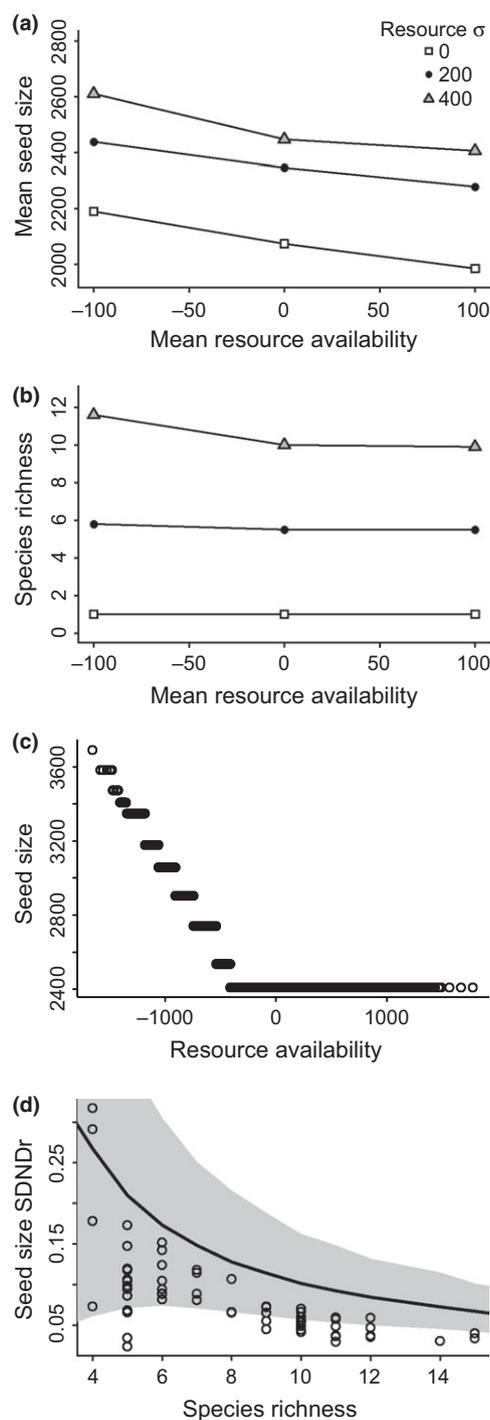
Figure 1 Simulations of coexistence based on a tolerance-fecundity trade-off linked to variation in seed size (see Box 1). (a) Across communities, mean seed size decreases with mean resource availability. (b) Local species richness depends on the within-community variation in resource availability. (c) The within-community relationship between seed size and resource availability. (d) Trait spacing patterns using a parametric approach: points represent observed values from the simulation, and the black line represents the mean of a null model that samples species irrespective of trait values. The grey area encloses the 2.5% and 97.5% quantiles of the null distribution. Points below the black line therefore indicate communities in which seed sizes were more evenly spaced than expected, but only points below the shaded area were significantly different from the null distribution (two-tailed test, $\alpha = 0.05$). 'SDNDr' is the standard deviation of nearest neighbour distances among co-occurring species, corrected for total trait range.

value determined by the environment and the species' actual trait values. The species with the trait value closest to the optimum will have the highest K and, all else equal, will exclude its competitors. Incorporating trait influences on niche partitioning is not as easy. To get coexistence, we need the α_{ij}'s to be sufficiently smaller than 1 to overcome the differences in the K's. In other words, species need to limit their own population growth more than they limit their competitor's population growth. The question is how particular functional trait differences cause species to have larger competitive effects on conspecifics than on heterospecifics. Returning to the previous example, why might the high SLA species limit its own population growth rate more than it limits the population growth rate of a low SLA species?

We can ask the same question using Chesson's (2000) concepts of relative fitness differences and stabilising mechanisms. In the hypothetical absence of stabilising mechanisms, relative fitness differences lead to competitive exclusion. For example, in the Lotka–Volterra model, if the α's are all equal, the species with the highest K will exclude the others. It is clear how trait differences can lead to relative fitness differences by creating differences in the K's. But how can trait differences create the stabilising forces necessary to offset those relative fitness differences and help a rare species rebound from low abundance in the face of competition? More specifically, since the α_{ij}'s will be exactly equal to the α_{ii}'s when species niches overlap perfectly, but will be less than the α_{ii}'s as niche overlap decreases, how can trait differences reduce niche overlap?

Perhaps, one set of traits acts on the K's to create competitive hierarchies, and a second set of traits acts on the α's and reduces niche overlap. For example, Swenson & Enquist (2009) found that variation in SLA and wood density was under-dispersed at small spatial scales in a tropical forest, consistent with the environmental filtering hypothesis, while seed mass values were over-dispersed, perhaps reflecting niche partitioning. However, we are sceptical that invoking distinct traits to drive environmental filtering and niche partitioning will provide a general solution. Any trait difference is likely to influence both processes, even if it has a stronger net effect on one (Kraft *et al.* 2008; Cornwell & Ackerly 2009). The high within-community variation of essentially all traits supports this view: a trait driving only environmental filtering, with no role in niche partitioning, should not only be under-dispersed relative to a null model but should have low absolute variance within a community (Westoby *et al.* 2002).

Our task is to explain how a difference in a particular functional trait reduces niche overlap. In a homogeneous environment with only one limiting resource and no trophic interactions, trade-offs and the niche differences they generate are impossible and trait variation could only create fitness differences. For example, in our seed-size simulation (Box 1), only one species can persist in the absence of local heterogeneity in resource availability. However, in the presence of local heterogeneity niche overlap is reduced because the habitat is partitioned on the basis of seed size: The largest seeded species has exclusive access to the most stressful microsites, while the smallest seeded species' fecundity advantage allows it to win high resource microsites. More generally, trade-offs and niche partitioning may arise not only from trait-based differences in species' responses to spatial environmental variation but also from differences in responses to temporal variation, multiple resource limitation or natural enemies.

SPATIAL HETEROGENEITY

Spatial environmental heterogeneity can reduce niche overlap and promote coexistence when different species are favoured in different local environments (Fig. 2a). Stronger differentiation in species responses to the environment leads to lower niche overlap, while the proportion of each environment on the landscape influence the K's (the species favoured by the more abundant habitat will have a competitive advantage). Although the concept is intuitive, rigorous mechanistic tests may strike readers as surprisingly complex. This complexity reflects the fact that for environmental heterogeneity to stabilise coexistence, and not simply reduce relative fitness differences, the direct effect of the environment on each species must interact with the net (intra- plus interspecific) effect of competition. A species' direct response to the environment, E, is measured by its overall fitness (per capita growth rate) or a fitness component (survival, growth, or fecundity) *in the absence of any competition* (Chesson 2000). The net effect of competition, C, is defined as E divided by the corresponding performance metric measured in the presence of intra- and interspecific competitors. For example, if $C = 2$, then the focal species' per capita growth rate decreases by a factor of two in the presence of competitors at their average densities. Coexistence is stabilised when E and C covary positively, meaning that species are most limited by competition in the environments where they are most favoured. This limitation of the most favoured species prevents it from excluding inferior competitors and, conversely, helps it to recover rapidly from low abundance by allowing for a strong competitive release. Scale is also an issue: For spatial heterogeneity to stabilise coexistence within a community, the spatial scale of the heterogeneity must be smaller than the scale at which the community is defined.

A rigorous trait-based test would show that the covariance between environment, E, and competition, C, increases with increasing functional trait differences between the focal species and the rest of the community. This test, which could be applied to any functional trait and either plant or animal communities, would show that more functionally unique species have population dynamics that are more stabilised by environmental heterogeneity. The challenge is measuring E and C for enough species to correlate the E-C covariance with functional trait differences. Removal experiments offer

one solution for measuring E and C. For species with simple life cycles, these experiments could measure the overall per capita growth rate (Sears & Chesson 2007), while experiments with long-lived species might be limited to measuring fitness components. An alternative solution is to use long-term demographic data sets to fit neighbourhood competition models (Uriarte *et al.* 2010) which then can be simulated to estimate fitness components, or even per capita growth rates, with or without competition (e.g. Adler *et al.* 2012).

Because the ideal test is logistically challenging, we consider less rigorous tests as well. One way to simplify the test is to focus entirely on the environmental response, E, setting aside the question of E-C covariance. Tests showing that the performance of species with different traits responds differently to environmental gradients (Fig 2b) would at least establish an important prerequisite for coexistence via environmental variation. Specifically, we would look for a positive correlation between species' pairwise trait differences and the differences in their response to environmental variation (Fig. 2c). The challenge, as mentioned before, is measuring a species' environmental response, E, in the absence of competition. It will be tempting to use local abundance as a proxy for E. However, realised abundances may be a poor indicator of environmental response because they also reflect the effects of competition (Fox 2012). A species that responds strongly and favourably to the environment in the absence of competition might be rare, or even excluded from the site entirely, in the presence of intra- and/or interspecific competitors. While patterns of abundance cannot be treated as direct measures of E, they may be useful in generating hypotheses to guide future, more rigorous research about individual-level environmental responses.

Empirical evidence

We found no field studies linking functional traits to species' responses to environmental variation in the absence of competition. However, many investigators have demonstrated correlations between functional trait values and patterns of species abundance or occurrence along environmental gradients (Díaz *et al.* 1998; Garnier *et al.* 2004; Cornwell & Ackerly 2009; Shipley 2010). In general, species with resource-acquisitive leaf economics traits, such as high SLA, short leaf lifespan and high leaf N and P concentrations,
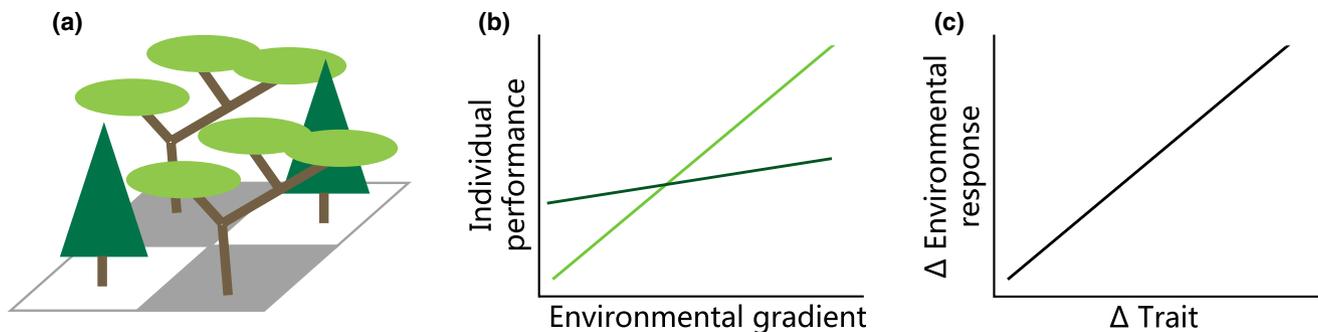

Figure 2 Spatial heterogeneity promotes coexistence when different traits are favoured in different environments. (a) High specific leaf area (SLA) species are often favoured on high resource patches (grey), while low SLA species are favoured on low resource patches (white). (b) A first step in testing the role of traits in coexistence is to describe how the individual performance of many species with different traits responds to the key environmental (or resource) gradient. Individual performance (i.e. fitness components) should be measured in the absence of competition. (c) Evidence that spatial heterogeneity operates on trait differences could come from a positive correlation between pairwise species trait differences and pairwise differences in environmental response [the difference in the slopes of the lines shown in panel (b)]. The sign of this correlation is more important than its slope, which will vary by community and trait.

occur more frequently or reach higher abundances in sites with higher water and/or nutrient availability. For example, Katabuchi *et al.* (2012) found that mean SLA and relative growth rate responded strongly to soil resource availability in a tropical forest, whereas seed mass and wood density were less responsive. Similarly, Mason *et al.* (2012) showed that increasing soil P in a New Zealand temperate forest favoured species with high leaf N and P.

Spatial heterogeneity created by patchy disturbances can also interact with trait variation. In moist tropical (e.g. Poorter *et al.* 2008; Uriarte *et al.* 2010) and temperate forests (Walters & Reich 1999; Lusk 2002), high SLA, resource-acquisitive leaf economics species are favoured in high-light gap environments and low SLA, resource-conservative leaf economics species are favoured in low-light, late successional environments. However, in some temperate communities of winter deciduous trees, high SLA species are more shade tolerant than low SLA evergreen species and are found in low-light environments (Jurik 1986; Janse-Ten Klooster *et al.* 2007). The contrasting relationships between SLA and light may be a function of leaf life span. In evergreen species, low SLA promotes shade tolerance by providing a long leaf life span, whereas in winter deciduous species, where leaf life span is constrained, high SLA provides an advantage in shade by increasing the leaf area (per unit leaf mass) for light capture (Janse-Ten Klooster *et al.* 2007; Lusk *et al.* 2008). Similarly, seed size can mediate differences in species responses to disturbance when small and large-seeded tree species have different germination cues, allowing them to specialise on forest gaps of different sizes (Pearson *et al.* 2002).

Stem traits such as wood density and vessel anatomy show similar patterns of variation across different environments. For example, wood density is often negatively correlated with soil fertility (reviewed by Chave *et al.* 2009), suggesting that resource-conservative strategies may be favoured in low resource environments. Differences in vessel anatomy have also been implicated in habitat use. Within angiosperms, species with diffuse-porous vessel anatomy have been found to dominate mesic and hydric sites, whereas species with more constrained (sectored) anatomy typically dominate xeric sites (Zanne *et al.* 2006). The underlying mechanism may involve a trade-off between the efficiency of hydraulic conductivity in well-integrated species vs. hydraulic safety in the face of drought in sectored species. Similarly, differences in xylem structure and function between conifers and angiosperms have long been hypothesised to give angiosperms a competitive advantage in most environments, restricting conifers to sites subject to drought and/ or freezing stress (e.g. Bond 1989; but see Pittermann *et al.* 2005).

Variation in seed mass also creates differential responses to environmental heterogeneity, as illustrated in Box 1. Large-seeded species tend to have higher seedling survival rates in sites where nutrient, water or light availability is low (Leishman *et al.* 2000; Dalling & Hubbell 2002; Coomes & Grubb 2003; Moles & Westoby 2004; Pakeman *et al.* 2008). This early life survival advantage might favour large-seeded species on low resource sites. On high resource sites, where both small and large-seeded species can thrive, small seeded-species might have a numerical advantage due to the trade-off between seed size and seed number (Smith & Fretwell 1974). Muller-Landau (2010) showed analytically that such a "tolerance-fecundity trade-off" can stabilise coexistence, and this theory has already received some experimental support (Ben-Hur *et al.* 2012). In effect, seed size mediates species' responses to an environmental gradient as in Fig. 1B.

Competition-colonisation trade-offs (e.g. Tilman 1994) are another spatial coexistence mechanism linked to variation in seed mass. Seed mass should have a positive effect on competitive ability and a negative effect on colonisation or dispersal ability (Rees & Westoby 1997; Kisdi & Geritz 2003). However, field studies indicate that competition-colonisation trade-offs are unlikely to be an important coexistence mechanism in natural communities because the required strict competitive hierarchy is often violated (Freckleton & Watkinson 2001; Coomes & Grubb 2003; Calcagno *et al.* 2006).

We have overwhelming evidence that trait variation influences species abundances and occurrences along spatial environmental gradients. Patterns of co-occurrence that show trait clustering due to unidentified environmental variation provide additional evidence for a role of traits in spatial environmental filtering (Kraft *et al.* 2008; Swenson & Enquist 2009; Wilson & Stubbs 2012). However, the utility of these results for testing spatial coexistence mechanisms is limited for two reasons. First, the spatial scale at which environmental variation is sampled is often coarser than the scale at which we seek to explain coexistence. We have good reasons to suspect that spatial heterogeneity also has strong influences at fine scales as well. For example, grassland species respond to subtle spatial variations in hydrology (Silvertown *et al.* 1999) and soil depth (Fridley *et al.* 2011). Unfortunately, these fine-scale responses are rarely linked to widely measured functional traits. The second, more serious, limitation is that variation in observed species abundances may be a poor proxy for variation in species' direct response to the environment (Fox 2012). We are not aware of any studies in natural systems in which the interaction between functional traits and spatial environmental variation was studied in the absence of competition, let alone studies of how trait differences may drive covariance between environment and competition.

TEMPORAL HETEROGENEITY

Chesson (2000) reviews two mechanisms by which temporal environmental fluctuations may promote coexistence, the temporal storage effect and relative nonlinearity. Under the storage effect, species may have similar responses to limiting resources, but each species is favoured at a different period of time (Fig. 3a). For example, annual plant species may differ in their germination cues, with some species germinating following warm rains, and other species germinating following cold rains (Levine *et al.* 2008). The greater the difference in germination timing, the greater the reduction in niche overlap, while the frequency of warm or cold rains influences the relative fitness differences. The storage effect receives its name because, to survive unfavourable periods, species must store the benefits of favourable periods in dormant seeds, diapause or long-lived adult stages. Like the tests of spatial coexistence mechanisms described previously, tests of the temporal storage effect rely on estimates of species' responses to the environment, E, and competition, C. The stabilising strength of the storage effect can be estimated by the shift in the environment-competition covariance that a species experiences when in invader vs. resident states (Chesson 2008). Strong E-C covariance will keep a resident species in check during favourable years, when it experiences strong intraspecific competition. On the other hand, if E-C covariance is weak when a species is in the invader state, it can increase rapidly from low density during favourable years.
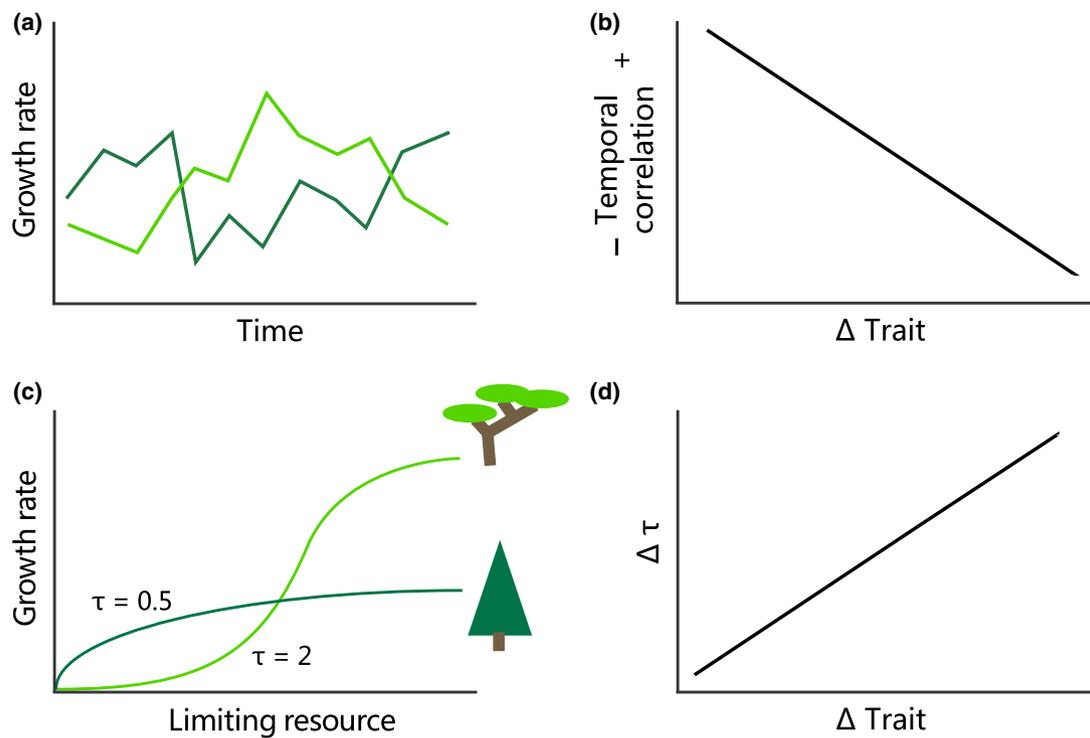
Figure 3 Temporal heterogeneity promotes coexistence through two mechanisms. (a) The temporal storage effect can operate when species responses to environmental fluctuations are less than perfectly correlated. (b) An initial test of the role of functional traits in driving the storage effect would relate species pairwise trait differences with temporal correlations in species responses; large trait differences should correspond with weak or negative temporal correlations. (c) Relative nonlinearity operates when species have different nonlinear responses to a limiting factor that fluctuates in time. In this hypothetical example, the reaction norms at low resource levels are given by x^τ, where τ is a measure of nonlinearity. (d) A trait-based test would show a positive correlation between functional trait differences and differences in nonlinearity, τ.

As in the spatial heterogeneity case, the most rigorous trait-based approach would predict that the magnitude of the invader vs. resident shift in E-C covariance should correlate positively with the difference in functional traits between the focal species and the rest of the community. More tractable, if less conclusive, trait-based tests could simply focus on differences in species responses to temporal environmental variation. If species respond identically to temporal fluctuations, then a storage effect is impossible. However, if species differ in the direction of their response to fluctuations (Fig. 3a) or their sensitivity to the environment (Chesson and Yuan unpublished data), then a storage effect becomes possible. A trait-based approach would predict that species pairwise correlations in temporal response should correlate with the magnitude of their functional trait differences (Fig. 3b). Again, we emphasise that the environmental response should be estimated by a fitness component, or per capita growth rate, measured in the absence of competition.

The second mechanism by which temporal heterogeneity can promote coexistence is via relative nonlinearity (Chesson 2000). Under relative nonlinearity, species are active at exactly the same times, but the reaction norms relating population growth rates to a limiting (competitive) factor take different shapes for different species. For example, population growth of a conservative life-history species might increase rapidly at low resource availability before reaching an asymptote at a relatively low maximum growth rate (Fig. 3c). In contrast, a species with a more resource-acquisitive life history may only respond weakly to increases in resources at low

ambient levels, but may achieve a higher population growth rate at high resource availability (Fig. 3c). If resource availability fluctuates, due to endogenous or exogenous forcing, the species with the conservative strategy will be favoured at times of low resource availability, while the more acquisitive species will be favoured at times of high resource availability. The mechanism stabilises coexistence because each species influences the pattern of resource availability in a way that favours its competitor. When the conservative species is most abundant and the acquisitive species is rare, resource pulses are poorly utilised; when the acquisitive species is most abundant and the conservative species is rare, resource pulses are quickly drawn down to a level where the conservative species has an advantage.

A trait-based test of relative nonlinearity would simply correlate trait differences with the parameter describing the degree of nonlinearity in the reaction norms. As trait differences increase, we should see increasing differences in nonlinearity (Fig. 3d).

Empirical evidence

While the storage effect has been the focus of considerable empirical work in terrestrial plant communities (e.g. Adler *et al.* 2006; Angert *et al.* 2009; Usinowicz *et al.* 2012), few studies have linked functional traits with species-specific differences in the timing of favourable conditions. Angert *et al.* (2009) provide an important exception, clearly linking leaf traits to the demographic variation driving a temporal storage effect in a community of

Sonoran desert annuals. They found that species with low leaf N, high SLA and high relative growth rates were favoured during the warm periods following large rainfall events while species with low SLA, but high leaf N were favoured during brief cool periods following small rainfall events. Thus, differences in leaf traits lead to differences in the timing of population growth [compare our Fig. 3b with Fig. 3 in Angert *et al.* (2009)]. On the basis of evidence that leaf N is adaptive under cold temperatures within a species' range (Weih & Karlsson 2001), and across species at regional and global scales (Körner *et al.* 1986; Reich & Oleksyn 2004), we speculate that interactions between leaf N and temperature fluctuations might drive temporal storage effects in other communities as well.

Although relative nonlinearity has received little empirical attention of any kind, we see great potential to link this mechanism with variation in functional traits. The theoretical example we described featuring resource-conservative and acquisitive species (Fig. 2c) maps directly on to the leaf economics spectrum. Species with short-lived, thin leaves with high concentrations of N and P might have a concave-up response to a limiting factor, like our hypothetical resource-acquisitive species, while species with high long-lived, thick leaves and low N and P might have a concave-down response, like our hypothetical resource-conservative species. The greater the difference in leaf economic traits between a pair of species, the more likely we are to find strong differences in the nonlinearity of their response to limiting factors (Fig. 3d). Likewise, there is growing evidence for a global wood economic spectrum (Chave *et al.* 2009) that also spans a resource-acquisitive (low density) to conservative (high density) axis. Therefore, relative nonlinearity might by mediated by either leaf or wood economic traits.

Variation in seed size might also generate different nonlinear responses to limiting factors. Small-seeded species have high relative growth rates and perhaps a concave-up response to limiting resources, while large-seeded species have lower relative growth rates and perhaps a more conservative strategy (Leishman *et al.* 2000). Consistent with this hypothesis, Coomes & Grubb (2003) speculated that small-seeded species could increase in abundance more quickly following a reduction in competition following a sequence of bad years. On the other hand, small-seeded species may have lower germination fractions (Pake & Venable 1996), which would limit their ability to respond rapidly to a reduction in competitive pressure.

RESOURCE PARTITIONING

Resource partitioning, which occurs when species differ sufficiently in the ratio of their resource requirements (Tilman 1982), can stabilise coexistence even in a spatially and temporally homogeneous environment (Fig. 4a). Stronger trade-offs in resource requirements lead to greater reduction in niche overlap, while resource supply rates influence the relative fitness differences (the species limited by the more abundant resource will have a competitive advantage). Many of the classic examples involve laboratory experiments with phytoplankton. In terrestrial plant communities, tolerance for low availability of a limiting resource is often a good predictor of competitive dominance (Miller *et al.* 2005) and trade-offs in resource requirements can promote species diversity (Harpole & Tilman 2007).

Trait-based tests of resource partitioning are conceptually straightforward. In resource partitioning models, the outcomes of competi-
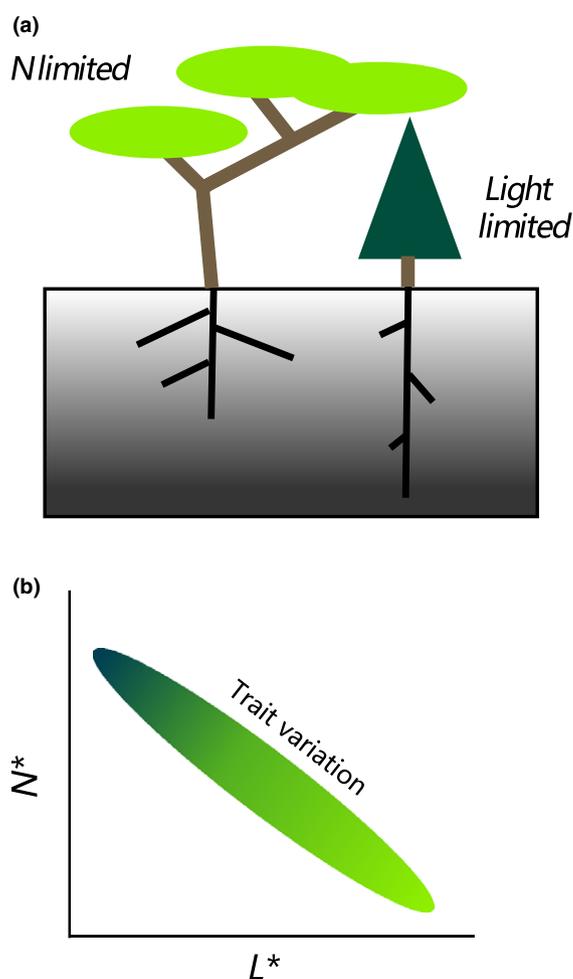

Figure 4 Resource partitioning can promote coexistence even in a spatially and temporally homogeneous environment when species are limited by different resources (a). A trait-based test would correlate variation in a functional trait with species tolerances (R^* values) to low levels of the limiting resources, nitrogen (N^*) and light (L^*) in this cartoon. (b) Evidence that variation in the trait drives a trade-off in R^* values for the two resources would link trait differences with coexistence.

tion are determined by species' R^* values, the lowest level of a resource at which a species can grow. Therefore, we simply need to correlate functional trait values with R^* values. If variation in a trait drives an R^* trade-off (Fig. 4b), meaning that higher values of the trait lead to a higher R^* on one resource but a lower R^* on another resource, then trait variation may stabilise coexistence (the outcome will also depend on resource supply rates and the species' stoichiometries). The challenge is determining the R^* values, typically done experimentally (e.g. Tilman & Wedin 1991). Somewhat weaker, but still valuable, evidence, would come from experimental manipulations of resource availability showing that changes in species abundances are consistent with predictions based on expected relationships between functional traits and R^* values.

Empirical evidence

Linking resource partitioning to leaf traits is complicated by the fact that species with rapid growth often have high requirements for many mineral resources (e.g. species with a high N requirement also

have a high P requirement). Similarly, species with large seeds are more tolerant of a wide variety of limiting factors. Depending on the resource supply rate at a site, we should expect to find either resource-acquisitive or conservative leaf economics species, or small or large-seeded species, rather than coexistence of both mediated by a trade-off in mineral nutrients. However, leaf economics could mediate a trade-off between light and mineral nutrients: conservative leaf economics species may have lower requirements for mineral resources, while acquisitive leaf economics species may have a lower requirement for light (Fig. 4).

Evidence that resource limitation favours conservative leaf economics species is easy to find (e.g. Reich *et al.* 1999). Similarly, fertilisation studies have shown that high N favours resource-acquisitive species (Suding *et al.* 2005; Laliberté *et al.* 2012). Evidence that light limitation favours resource-acquisitive leaf economics species is harder to find. Studies in moist tropical forests and temperate rain forests in Chile actually show the opposite pattern: late successional, shady environments favour low SLA species, not high SLA species (Kitajima 1994; Lusk 2002; but see Gianoli & Saldaña 2013). Therefore, the potential for leaf economics to mediate a trade-off between nutrient limitation and light limitation might be restricted to those temperate systems where the shade tolerant species have high SLA (Jurik 1986; Janse-Ten Klooster *et al.* 2007; Lusk *et al.* 2008).

Consistent with a trade-off between nutrient and light limitation, Gross *et al.* (2007) found that competition within functional groups was more intense than competition between functional groups in a fertilised temperate grassland, and proposed a light vs. N trade-off between high and low SLA species as the underlying mechanism. Dybzinski & Tilman (2007) investigated a trade-off between light and N limitation among temperate grassland species, and found that it was consistent with coexistence in two of the eight species pairs they studied. However, based on SLA values reported in a related paper (Tjoelker *et al.* 2005), differences in SLA are not related to this light-N limitation trade-off. Moreover, this mechanism requires predictable differences in another trait, plant height. The better competitor for soil resources (conservative leaf economics species) must be shorter than the better competitor for light (acquisitive leaf economics species). If the soil resource specialist is not shaded by a taller competitor, it will draw soil resources down to levels that exclude the light-specialist (Dybzinski & Tilman 2007). Future trait-based research on this trade-off should focus on root–shoot ratios.

NATURAL ENEMIES

Natural enemies, including pathogens, predators and herbivores, can promote coexistence in many ways (Chesson 2000; Chesson & Kuang 2008). Different species may be kept in check by different specialist natural enemies (Janzen 1970; Connell 1971), and generalist herbivores can stabilise coexistence through frequency-dependent functional responses (prey switching) (Murdoch & Bence 1987). Recent work in plant communities has highlighted soil pathogens as a particularly powerful source of conspecific density-dependence with great potential to stabilise coexistence (e.g. Klironomos 2002; Mangan *et al.* 2010). However, while coexistence based on species-specific enemies makes intuitive sense in classic coexistence tests focused on distinct species, it may not apply to coexistence tests based on continuous variation in widely measured plant functional
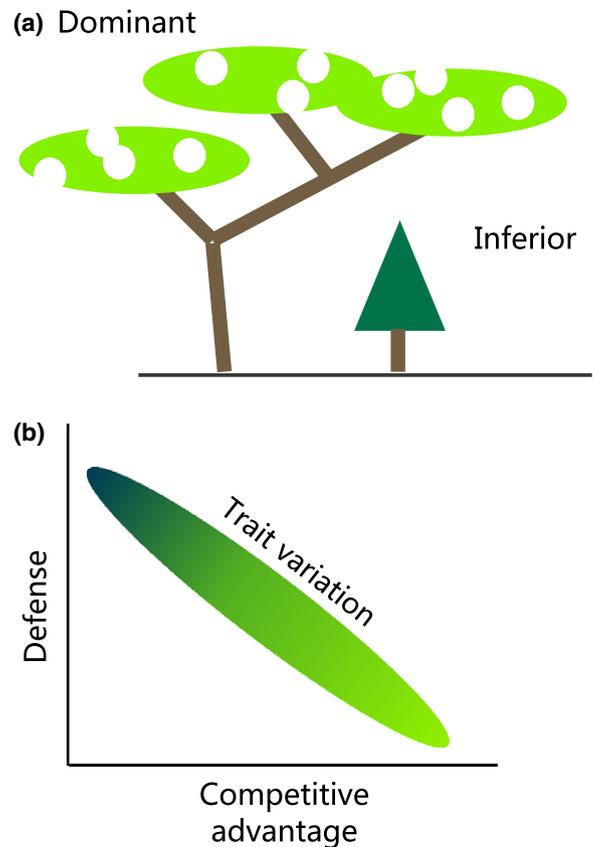

Figure 5 Herbivores may interact with trait variation to promote coexistence when (a) herbivory prevents poorly defended, dominant competitors from excluding well-defended, inferior competitors and (b) a functional trait mediates a competition-defence trade-off.

traits. Although the presence or absence of particular plant defence compounds could influence specialist herbivores, the leaf, wood and seed traits discussed here are more likely to influence the probability of attack by generalist herbivores (e.g. Tanentzap *et al.* 2011) while having little impact on species-specific enemies.

On the other hand, in environments where poorly defended species are at a competitive advantage, the presence of herbivores could prevent them from excluding better defended plants (Holt *et al.* 1994). This competition-defence trade-off (Viola *et al.* 2010) can be stabilising as long as the herbivore populations are coupled to the population size of vulnerable plants. A trait-based test would show that variation in a functional trait is related to both defence and competitive dominance (Fig. 5).

Empirical evidence

Leaf economics can play an important role in understanding the vulnerability of species to generalist herbivores. Resource-acquisitive species have low structural resistance and are often preferred by herbivores due to their high palatability (e.g. Kitajima 1994; Wright *et al.* 2004; Tanentzap *et al.* 2011). Differences in leaf economics could promote stable coexistence in high resource sites where herbivores prevent resource-acquisitive species from excluding resource-conservative species (Fig. 4). For example, Quétier *et al.* (2007) found that fertilisation of a French subalpine grassland favoured

high SLA species, while grazing increased the abundance of unpalatable species with tough leaves. Eskelinen *et al.* (2012) also provide evidence that aboveground traits mediate a trade-off between herbivore defence and resource competition. Within infertile plots where average tissue C:N ratio was high, indicating low palatability, herbivores decreased plant diversity, whereas in fertile plots where average C : N ratio was low, herbivores increased diversity. Wood density may interact with natural enemies in similar ways. Higher wood density is typically associated with greater resistance to natural enemies (animals and fungal pathogens), slower growth rates and reduced mortality rates (Chave *et al.* 2009; Kraft *et al.* 2010). Under high resource conditions where these slow growing, high wood density species might be at a competitive disadvantage, natural enemies could help maintain diversity by reducing the abundance of fast growing, low wood density competitors.

We were surprised to find many empirical studies demonstrating the opposite pattern, with resource-acquisitive species increasing in abundance with grazing or mowing, and resource-conservative species decreasing in abundance (Díaz *et al.* 2001; Laliberté *et al.* 2012). In this case, differences in tolerance to herbivory appeared to be more important than differences in palatability and herbivore preference. The key point is that while the resource-acquisitive species may be palatable, they also quickly replace lost leaf tissue. Thus, in systems dominated by plants with resource-conservative traits (e.g. large prairie bunchgrasses with low SLA and high leaf C : N; Garnier *et al.* 2004; Fargione & Tilman 2006), herbivory may promote the persistence of resource-acquisitive species that might otherwise suffer competitive exclusion. However, because generalist grazers can feed on both types of species, the intensity of herbivory is not tightly coupled to the density of either one, as it would be in the previous case where herbivores specialise on the resource-acquisitive species. The lack of density-dependent feedbacks means that this is not a true stabilising mechanism; it will slow competitive exclusion but cannot prevent it (Chesson 2000).

Seed size could also mediate a competition-defence trade-off. In stressful or low resource sites, large-seeded species will have a competitive advantage at the establishment stage (e.g. Leishman *et al.* 2000; Coomes & Grubb 2003). On the other hand, large-seeded species are often more vulnerable to predators (Harper *et al.* 1970; Mittelbach & Gross 1984; Boman & Casper 1995), although in some systems the correlation between seed size and seed predation is weak or even negative (e.g. Moles *et al.* 2003). Furthermore, correlations between seedling performance and seed size weaken rapidly after the early seedling stage (Dalling & Hubbell 2002). We did not find any experimental studies showing that herbivore exclusion altered the outcome of competition between large and small-seeded species.

TESTING THE COMBINED EFFECTS OF MULTIPLE MECHANISMS

Although we have treated each category of coexistence mechanism separately, in real plant communities we expect many mechanisms to operate simultaneously. In fact, coexistence is likely to involve trade-offs among many axes of trait variation or resource limitation (Clark *et al.* 2010). Phenomenological approaches, which focus on the demographic signature of stabilising niche differences, may be the best way to estimate the combined effects of multiple mechanisms (Adler *et al.* 2007). For instance, Uriarte *et al.* (2010) showed that individual trees surrounded by neighbours with traits dissimilar to their own outperformed individuals surrounded by neighbours with similar traits. By combining this approach with the mechanistic tests we are advocating, investigators can evaluate the importance of a particular coexistence mechanism relative to the net effect of all stabilising niche differences.

FUTURE DIRECTIONS

Identifying when and where particular coexistence mechanisms are most important is an essential first step towards predicting the effects of global change on biodiversity. In principle, all four classes of coexistence mechanisms that we considered could act on functional trait variation to reduce niche overlap and promote diversity. However, our review indicates that some mechanisms appear likely to be stronger and more widespread than others.

Spatial heterogeneity

Many studies have shown that at broad scales different sites favour different species based on their functional traits. The commonness of these trait-environment correlations suggests a high potential for interactions between spatial environmental heterogeneity and trait variation to stabilise coexistence. Rigorous tests of this mechanism should be the top priority for future research on traits and coexistence. The ideal test would measure environmental heterogeneity at fine, within-community scales and would quantify species' responses to the environment in the absence of competition. This research will be especially important in ecosystems where land-use and land management has altered spatial heterogeneity. Spatial heterogeneity also interacts with traits of non-sessile organisms, but the difficulty of determining the spatial scales over which mobile individuals interact will complicate tests of the mechanism.

Temporal heterogeneity

We see a strong theoretical case that temporal fluctuations in limiting factors could act on variation in leaf economics or seed size to stabilise coexistence through relative nonlinearity, but we could not find relevant empirical studies. Another fluctuation-dependent mechanism, the temporal storage effect, might be generated by interactions between leaf N and temperature. Both mechanisms offer promising opportunities for trait-based research.

Natural enemies

Pathogens, herbivores and predators have the greatest potential to stabilise coexistence when their impact on prey is species-specific, but we struggled to understand how variation in these functional traits could lead to strong, species-specific effects. When trait variation does not lead to species-specific enemies, both theory and field studies suggest that it can still stabilise coexistence through trait-mediated competition-defence trade-offs, but only under narrow ranges of resource supply rates, which is why we give this mechanism lower priority for future research.

Resource partitioning

Although resource partitioning is undoubtedly an important coexistence mechanism, we see limited potential to link it with commonly measured plant functional traits. Leaf and root economic traits can lead to a trade-off between N and light limitation, but this trade-off may only stabilise coexistence for narrow ranges of N supply rates. Resource partitioning should be a higher research priority in com-

munities of consumers with access to many food resources in many forms (e.g. Grant & Grant 2006).

A trait-based approach to coexistence represents a working hypothesis that interspecific trait variation interacts with environmental variation, resource availability and natural enemies in general, consistent ways across communities. Our hypothetical figures show the data required to test this hypothesis. For example, differences in species responses to environmental variation should correlate with differences in their traits in a similar way in many ecosystems (Fig. 2c). An alternative hypothesis is that the links between trait variation and coexistence are idiosyncratic and community-specific, implying that the relationships revealed by our proposed figures would vary dramatically among communities. For example, fertile microsites might favour high SLA species in some, but not most, communities. If trait-based coexistence is community-specific, we could still predict future biodiversity changes in well-studied systems, but our hope for a general and predictive trait-based approach to coexistence would be diminished. A final hypothesis holds that the bivariate trade-offs depicted in our figures are rare; instead, diversity is maintained by high-dimensional trade-offs involving multiple axes of variation in traits and complex interactions between individual performance and the environment (Clark *et al.* 2010). Failure to find evidence for the simple relationships between trait differences and performance differences that we have proposed would support this hypothesis. Given the current state of knowledge about functional traits and coexistence, rejecting any of these hypotheses would be premature.

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AUTHORSHIP STATEMENT

PBA and AF designed the project, PBA and NJBK performed the simulation analyses and all authors contributed to the literature review and writing of the manuscript.

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