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perspective

Individual variation and weak neutrality as determinants of forest diversity

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Abstract. Niche-based and neutral processes are alternative mechanisms proposed to maintain the diversity of forest trees. Neutral processes, meaning those that do not invoke fitness differences between species, have been discounted because of their central assumption of species equivalence. We propose weak neutrality as an alternative conceptual basis for the maintenance of diversity that does not require strict species equivalence. Weak neutrality is based on three underlying assertions. (1) Individual variation leads to broad species overlap, reduced rates of competitive exclusion, and forest dynamics that approximate a biased random walk. (2) Environmental variation results in stochastic spatial and temporal fluctuations in the magnitude and direction of the biased random walk, reducing the likelihood of fixation of a species and corresponding exclusion of others. (3) Limited dispersal in conjunction with environmental variation inhibits divergent evolution and increased niche separation. We suggest that the importance of weak neutrality as a determinant of diversity depends on the magnitude of both individual and environmental variability. Niche-based processes are expected to be more prominent along steep environmental gradients, in landscapes with environmentally heterogeneous patches, and across broad spatial extents along shallow environmental gradients. We distinguish weak neutrality from pure neutrality and other conceptual models of species diversity.

Keywords: diversity, forest dynamics, neutrality, niches, species richness, trees

Introduction

Delineating the mechanisms that maintain the diversity of forest trees has been a central but elusive problem in forest ecology. One longstanding explanation has been that tree species partition environmental variation into niches; tree species can co-exist in a forest if they differ sufficiently in traits important to the utilization of limited resources (e.g., Grubb 1977, Wright 2002, Silvertown 2004). Tradeoffs in fitness traits are presumed to result in a species having a competitive advantage under some set of environmental conditions (e.g., micro-environments), which together define that species' niche. As a result, deterministic selection of species relative to the suite of environmental conditions is expected to drive community dynamics and patterns of species diversity (e.g., Vellend 2010). The diversity of forest trees would then depend on the breadth and overlap of species' niches as well as the spatial and temporal distribution of micro-environments (e.g., Comins and Noble 1985, Pacala and Tilman 1994).

Niche partitioning in forest trees has been closely associated with variability in understory light levels that is, in turn, largely driven by canopy gap dynamics. Sunlight is a limiting resource in forest understories, and low light levels beneath the canopy mean that even the most shade-

The photograph shows (from the left) William Platt, Louis Gross and Brian Beckage at Beckage's lab on October 2011. Personal webpages: LG—http://nimbios.org/personnel/gross; WP—http://www.biology.lsu.edu/faculty_listings/fac_pages/bplatt.html; WG—http://www.biol.canterbury.ac.nz/people/godsoe.shtml; DS—http://eeb.bio.utk.edu/simberloff.asp

tolerant forest trees require increased light to reach the forest canopy (Canham 1989, Poulson and Platt 1996). When overstory trees are damaged or die, openings are created in the forest canopy; these canopy gaps are associated with elevated and spatially variable understory light levels (Runkle 1981, Poulson and Platt 1989, Canham et al. 1990). Propagules or advance recruits of trees colonize areas before and after canopy gap formation (e.g., Schupp *et al*., 1989). Seedlings and juveniles subsequently compete, often intensely, for vertical position to capture sunlight and to ultimately gain direct access to sunlight through entry into the forest canopy (e.g., Peet and Christensen 1987, Schupp et al. 1989, Purves and Pacala 2008; but see Paine et al. 2008 for evidence that this competition may sometimes be weak). Competition among forest tree recruits for access to light and canopy gaps is pre-emptive: seedlings established earlier in prior disturbances or in different types of subcanopy gaps (Connell et al. 1997) tend to have a competitive advantage over later arriving individuals because of their greater initial height and subsequent shading of competitors (Schwinning and Weiner 1998, Kwit and Platt 2003). Trees have unrestricted access to sunlight once they enter the canopy, and subsequently interact weakly with other canopy trees, even for below-ground resources (e.g., Wilson 1993), while strongly suppressing recruits of both the same and different species through shading The gap dynamic paradigm is generalizable to many plant communities and has broad application to closed-canopy forests worldwide (e.g., Platt and Strong 1989).

Broad empirical support for niche partitioning among forest trees has been lacking despite the importance of the gap-dynamic paradigm. The lack of support occurs even though there are known differences among tree species in use of light and other resources as well as in life history traits (e.g., Batista and Platt 2003, Beckage and Clark 2003, Condit et al. 2006, Ibanez et al. 2009). Instead, extensive empirical studies of forest dynamics have found strong evidence of large individual variability and broad species overlap in performance (e.g., Clark et al. 2004). Overlap among species in fitness traits ultimately results from demographic constraints and equalizing tradeoffs that characterize individual trees. Individuals must allocate a finite pool of fixed carbon, and more allocation to one fitness trait necessarily means less to another trait, e.g., those that enhance colonization versus competitive ability (Tilman 1988, Wright 2002). Resulting allocation patterns vary among individuals within species as well as across species and lead to species overlap in fitness traits (Clark 2010). Broad overlap among forest tree species suggests that existing explanations of niche partitioning among species are inadequate to explain the diversity of trees in forests.

One alternative explanation is that high individual variability in performance is evidence that niche partitioning occurs largely among individuals rather than species (Clark 2010). If individuals within species exhibit considerable variation in fitness traits, then tradeoffs manifested across individuals could provide the basis for niche partitioning of the environment. A niche would then be defined by the region in multidimensional space occupied by individuals of a given species, and the resultant hyper-dimensional niche would be difficult (or impossible) to measure fully (Clark et al. 2007). Species would be separated in this hyper-dimensional niche space, but would have apparently broad overlap when observing only a subset of that space (Fig. 1). This proposed explanation would reconcile empirical evidence of broad species overlap with niche partitioning, but is also 'unfalsifiable' as any observed species overlap could be interpreted as implying that an unspecified dimension of niche space was not measured.

Weak neutrality

We propose another interpretation of broad species overlap as evidence of 'weak neutrality'. Weak neutrality asserts that species dynamics are characterized by a biased, stochastic walk towards fixation (Beckage et al. 2010). Broad species overlap implies that the species identity of the individual that captures a given canopy gap is largely unpredictable and that the role of deterministic species selection is therefore relatively weak (Fig. 2) (Vellend 2010). Species overlap is not expected to

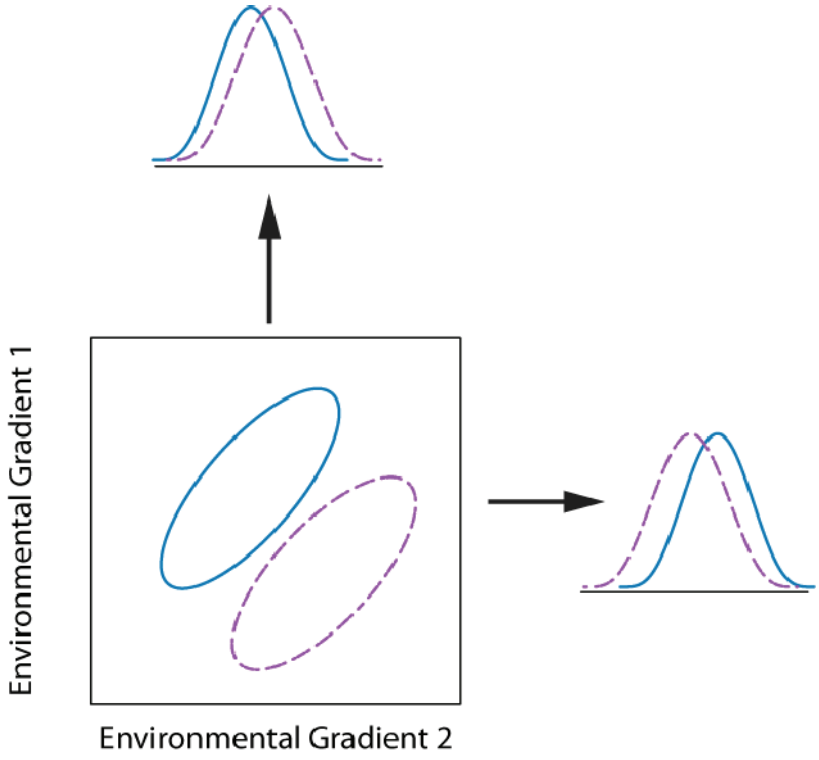

Figure 1. Separation of species in a hyper-dimensional space can lead to apparent species overlap in lower-dimensional space. Two hypothetical species (blue solid line and magenta broken line) are separated in two-dimensional niche space but appear to overlap in a single dimensional that marginalizes over the second dimension.

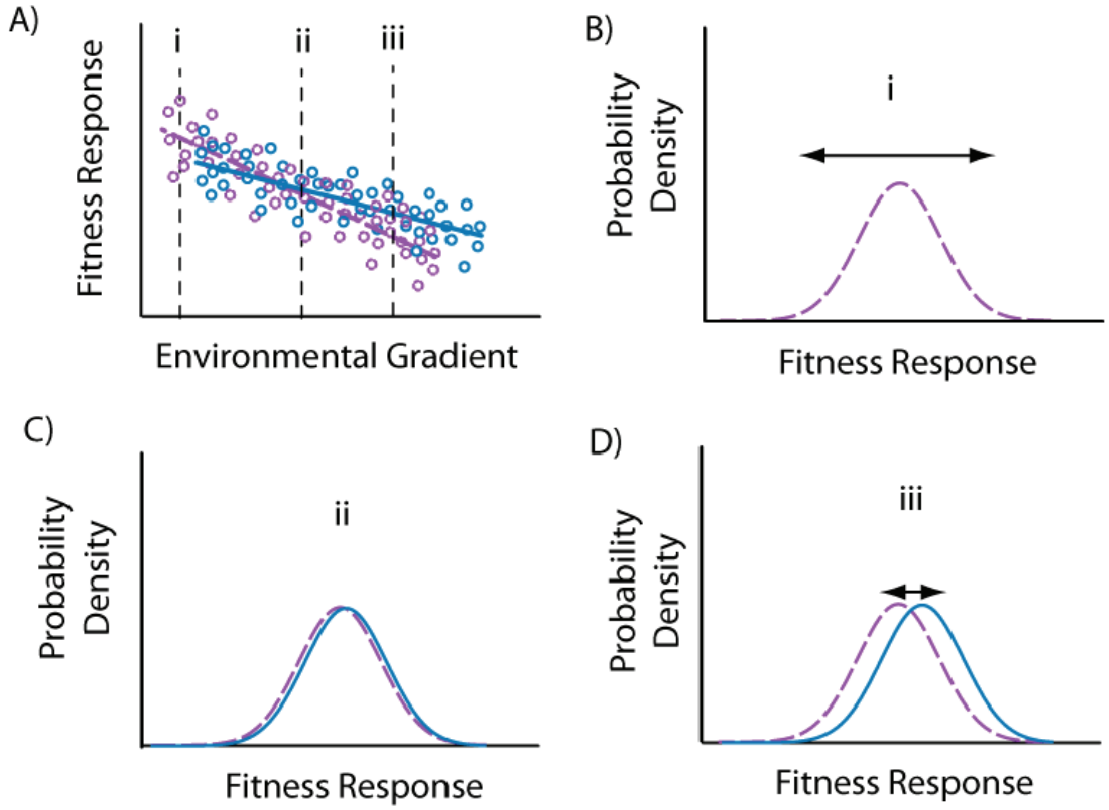

Figure 2. Individual variation in demographic traits influences the probability that a given species captures a site under a given set of environmental conditions. A) Hypothetical fitness responses of two species (blue and magenta) with respect to an environmental gradient. B)-D) represent the distribution of fitness responses of individuals of each species in environments i-iii in panel A. Each species dominates the other species at either end of the environmental gradient, but large individual variation results in broad overlap under intervening environmental conditions. The arrow in panel B represents the range of individual variation for the magenta species under environment i, while the arrow in panel D represents the difference in fitness response (or bias) between the two species distributions.

be exact, however, as species are not precisely equivalent and the mean difference between pairs of species is the bias favoring one species over another in a given environment. The bias represents the degree of niche separation (i.e., difference in selection probability) between species under a given set of environmental conditions. The resultant forest dynamics, reflecting both release and capture of canopy space through mortality and recruitment, approximates a random walk (i.e., drift) with both deterministic and stochastic components (Beckage et al. 2010). Species overlap represents the stochastic component of the random walk, while the bias represents the deterministic (niche partitioning) component (Fig. 2). The rate of competitive exclusion is reduced as the bias decreases or as the species overlap increases, approaching the process of ecological drift (e.g., Ågren and Fagerström 1984, Brokaw and Busing 2000, Vellend 2010). If the bias is small relative to individual variability, then species coexistence can result over ecological time scales, because a reduced rate of competitive exclusion means that long time periods are required for weaker competitors to be driven to local extinction. We additionally assert that the magnitude and direction of the bias fluctuates in space and time in response to environmental variation, so that the bias itself is stochastic and, thus, the random walk is unlikely to reach fixation on ecological time scales. Community dynamics can thus be approximately ('weakly') neutral without requiring strict species equivalence. This broad overlap can also be consistent with mean species differences, i.e., differences that can be statistically significant but still characterized by broad overlap. Species richness and diversity of the forest community is then an emergent property that results from the sum of the separate competitions for canopy gaps, which is in contrast to the deterministic community structure implied by niche partitioning.

We delineate two main sources of individual variation that contribute to species overlap in fitness attributes (Fig. 3). One is genotypic variation that results from alteration of haploid and diploid generations, and which includes the random segregation and assortment of genes in gametes and their subsequent recombination. The unpredictability of pollen transport by wind or animal vectors can also contribute to the genotypic variation of the subsequent generation of individuals. The second source of individual variation (i.e., phenotypic variation) results from variation in the local environmental conditions experienced by individuals. Environmental variation is expressed through a reaction norm influencing phenotypic expression of a given genotype (e.g., phenotypic plasticity) as well as through the differential fitness of individual genotypes in a given micro-environment. These sources of variation together result in observed intraspecific variation that has both a genetic and environmental component.

We contend that large individual variability in fitness traits within species and resultant broad species overlap can be maintained by the coincidence of environmental variation and dispersal limitation. Divergent evolution could lead to reduced niche overlap, with species residing in unique regions of trade-off space, such that each species is the best competitor under some set of environmental conditions (i.e., its niche; Levins 1968). Divergent evolution that increases niche separation of species can, however, be inhibited by unpredictable environmental variation in space and time in conjunction with inherent limitations on seed production and the stochasticity of seed dispersal (Hubbell and Foster 1986, Eldredge et al. 2005). The spatial distribution of micro-environmental conditions (e.g., niche space) across a community is likely to vary at short spatial and temporal scales (i.e., environmental grain; Levins 1968), resulting in a rough fitness landscape. The fitness of a given genotype would correspondingly be characterized by peaks and valleys on fine spatial scales. The fitness of an individual in this landscape would thus be likely to shift rapidly in time in response to environmental variation. For instance, interactions between moisture availability (e.g., variability in precipitation events), temperature (e.g., passage of warm or cold fronts), and magnitude of direct vs. indirect exposure to sunlight (e.g., clear or cloudy day,

sunflecks) as well as interactions with other species (e.g., seed predators, herbivores, pathogens, other plants, etc.) could result in fine scale temporal variation in fitness. Thus, the landscape is rugged across space and 'dancing' in time with respect to both the fitness of a given genotype and the dynamics of species. The pre-emptive nature of competition among forest trees together with the unpredictable nature of the 'fitness terrain' that a dispersing individual is likely to experience limits the potential for species to specialize in narrowly defined niches (or optimize traits, e.g., Levins 1968, Brown and Pavlovic 1992, Clune et al. 2008). The individual with the maximum fitness for a given environment is not likely to arrive at a location that maximizes its fitness, because arriving a fraction of a meter away or a day later can negate its fitness advantage (cf. elm-oyster model, Williams 1975). Species, in fact, often capture sites by default because of recruitment limitations (e.g., Hurtt and Pacala 1995). Species are generally not able to explore fully the spatial distribution of niches in a rugged, dancing landscape. The optimum fitness landscape in trait space, thus, is more

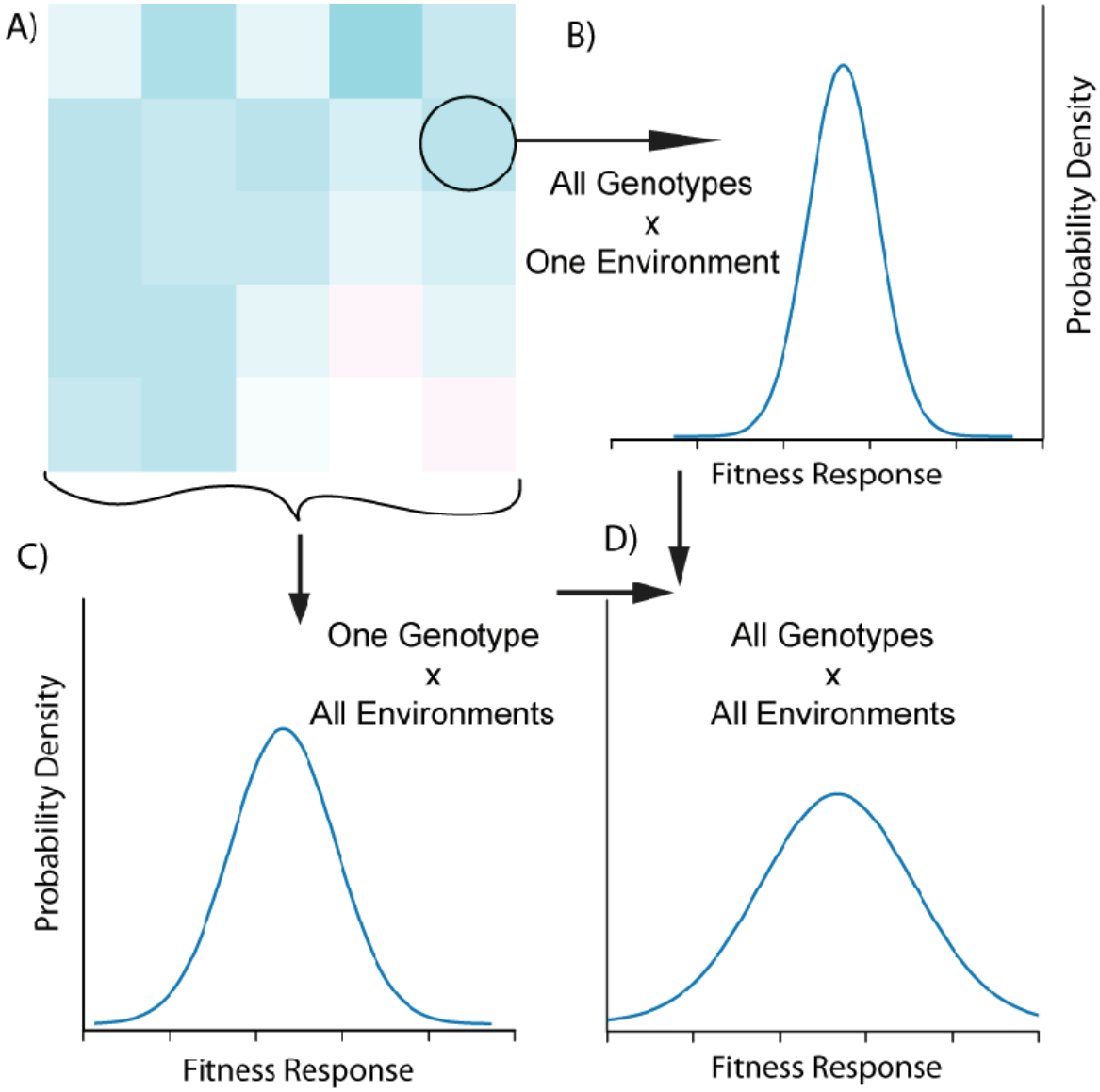

Figure 3. Individual variation in fitness attributes results both from genotypic and environmental variability. A) Spatially continuous environmental variation is discretized at the scale of the individual such that one individual can occupy one square. The fitness response of an individual varies with genotype (B) and environment (C). Panel B shows the variation in fitness across genotypes in a given environment, while panel C shows variation in fitness across environments for a single genotype. These two sources of variation in combination increase species' variability in fitness responses (D).

likely to be characterized by a broad plateau rather than a sharp peak.

We predict that the relative importance of weak neutrality in structuring community dynamics will vary with the magnitude of environmental and individual variation. Increasing environmental variation relative to individual variation will increase the bias (i.e., deterministic species selection) of the random walk resulting in more rapid competitive exclusion. Thus, weak neutrality will be more important in relatively homogeneous environments or across shallow environmental gradients (Fig. 4) because individual variation is more likely to exceed environmental variation. Niche differences can, however, be important even across shallow environmental gradients when considering species from across a sufficiently broad spatial extent (Fig. 4), for example, from disparate locations along a latitudinal temperature gradient. Increasing environmental heterogeneity that is spatially structured and thus somewhat predictable at the scales of tree dispersal (e.g., in steep environmental gradients such as a mountain slope) will result in increasing importance of niche processes as environmental variability overwhelms individual variability. There is greater support for niche partitioning in large canopy gaps, for instance, where environmental variation is relatively greater than in small canopy gaps (e.g., Poulson and Platt 1989; Whitmore 1989), while studies in more homogeneous environments offer little support for niche partitioning among trees (e.g., Gravel et al. 2008). Similarly, niche differences are expected to be increasingly important across broad geographic regions with corresponding larger environmental differences (Fig. 4). Temporal variation may operate in a similar manner to spatial heterogeneity, changing the magnitude and direction of the bias of the random walk to fixation (e.g., Beckage and Clark 2005), although perhaps with less capacity to influence species coexistence than purely spatial variation (Snyder 2008).

The importance of neutral processes in structuring forest dynamics has been largely discounted in ecology. Clark (2009), for example, argues that neutral models rely on stochasticity for coexistence, and that stochasticity is a reflection of a lack of information rather than a mechanism (Clark et al. 2007). This strictly deterministic view of ecological interactions, however, may be overly simplistic. If each species was dispersed to all microsites, then the best adapted individual for a given niche might reasonably be expected to capture a particular niche throughout the landscape, and a deterministic view of forest recruitment might be appropriate. But this is typically not the case because of dispersal limitations and environmental variability. While stochasticity is sometimes a proxy for unidentified deterministic (i.e., niche) processes (Clark 2009), the inclusion of stochasticity to account for genetic variation, dispersal, and environmental variation represents unpredictability that is 'real' rather than simply standing in for unidentified determinism in niche space. Purves and Turnbull (2010) maintain that it is exceedingly unlikely that species would display perfectly equalizing fitness trade-offs, and that pure neutrality is thus unlikely to be an important determinant of species diversity in forests. Model simulations do, in fact, show that even small departures from strict neutrality in the absence of environmental heterogeneity result in dramatic declines in species richness (Zhou and Zhang 2008). In weak neutrality, we instead assert that the magnitude of departures from strict neutrality (fitness differences) are relatively small with respect to individual variation, and that their magnitude and direction stochastically vary across space and time. Species dynamics are then only approximately neutral on average over ecological time scales, and rapid fixation of any given species is prevented by species overlap together with the changing bias of this random walk.

The importance of intraspecific individual variation in promoting species coexistence has been disputed. Lichstein et al. (2007) investigated the potential for individual variation to maintain species coexistence and found that the stabilizing effect of intraspecific variation on species coexistence was weak, because the species with the higher fitness will almost surely capture a given site as fecundity increases. In their simulations, species with small mean differences can still have

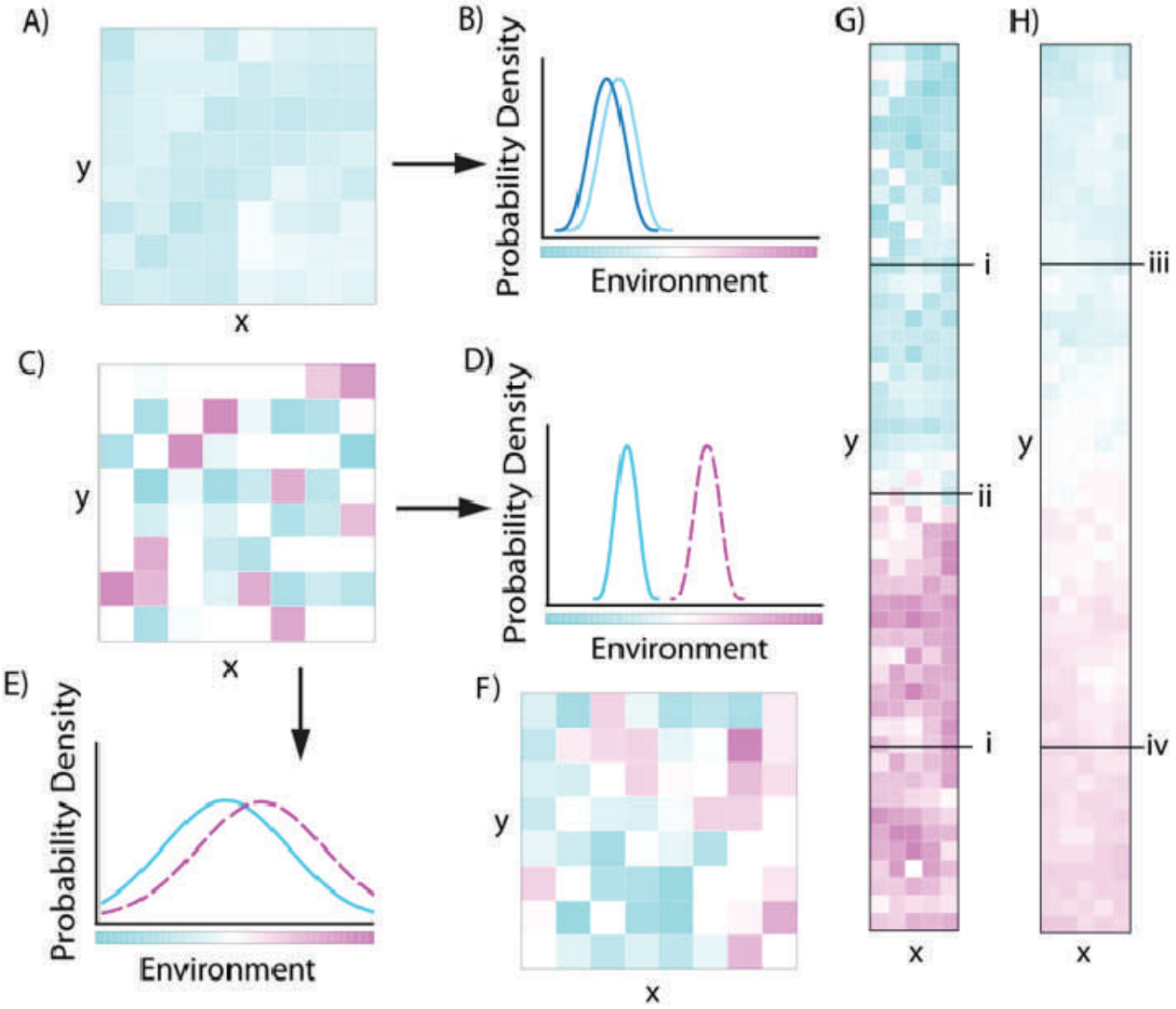

Figure 4. Individual variation in fitness attributes that is relatively large with respect to environmental heterogeneity can result in broad species overlap and approximately neutral dynamics. The magnitude of individual and environmental variation influences the relative importance of weak neutrality. More homogeneous environments (A) facilitate broad species overlap (B) and dynamics that are weakly neutral. Increasing environmental heterogeneity (C) favors niche separation (D) but can still allow for weakly neutral dynamics if individual variation is large and resultant species overlap is broad (E). Niche processes are thus likely to be more important in heterogeneous environments with spatial structure (F) at the scale of individuals, which increases the predictability of the environment with respect to species dispersal. We also expect the importance of neutral processes to vary at broader spatial scales associated with environmental gradients (G): Weak neutrality is expected to be more important in more homogeneous areas (i) with relatively low environmental variation and less important in ecotonal areas or regions with steep environmental gradients (ii). H) Niche differences can be important even across shallow environmental gradients when considering community differences across a sufficiently broad spatial extent (iii vs. iv). Note that we represent environmental variation spatially using colored squares discretized at the scale of the individual so that each cell can be occupied by a single individual. The x and y labels represent the spatial dimensions of the landscape. We represent hypothetical species with different colors and line types, and environmental suitability for these species using similar shades of color, e.g., light and dark blue, in the landscapes.

very large differences in the tails of the distributions, and eventually some individual (seed) will be drawn from the tail of the distribution with a greater fitness than its competitor. One implication is that there is variance-mean trade off in fitness: at high levels of seed production, species with higher variance are favored, but at lower levels of seed production, species with a higher mean are favored (Lichstein et al. 2007). Thus, a competition-colonization trade-off may also imply a corresponding trade-off in mean and variance of individual variation in fitness traits; 'colonizers' (with high fecundity) would benefit from high individual variation in fitness while 'competitors' (with low fecundity) would benefit from a high mean fitness. Their study, however, did not consider trade-offs between competitive performance and fecundity, so that the optimum individual can almost surely disperse to each available site. Courbaud et al. (2010) begin to consider such trade-offs and show the potential for individual variation to have large effects on species coexistence and patterns of abundance. The implications of individual variation have thus begun to be explored, but the demographic processes considered have been limited and have not yet included consideration of broader and more mechanistic trade-offs, the heritability of individual variation, priority effects, the separation of genotypic variation from phenotypic plasticity and environmental variation, or more complex communities (e.g., those with more than two species).

Weak neutrality, niches, and neutrality

We propose weak neutrality as an alternative model of forest dynamics that contains aspects of both niche models and pure neutrality. We make three key assertions in this conceptual model of forest dynamics: 1) Intraspecific (i.e., individual) variation in fitness traits results in broad species overlap with uncertain competitive outcomes, reduced rates of competitive exclusion, and forest dynamics that are characterized by a biased random walk. The bias of the random walk is the niche separation or mean fitness difference between species pairs. Both larger species differences and smaller intraspecific variation result in increasing departures from pure neutrality. 2) The magnitude and direction of the bias of the random walk (i.e., how strongly a given species is favored) fluctuates in response to spatial and temporal environmental variation. The identity of the species that is competitively favored, thus, varies both in space and time. This shifting bias of the random walk reduces the likelihood of species fixation or competitive exclusion. 3) Individual variation and species overlap are maintained by the unpredictability of fine scale environmental variation in conjunction with the stochastic nature of dispersal and inherent limits on fecundity. The optimal trait combination that maximizes fitness is likely to vary at fine spatial and temporal scales in response to changing micro-environmental conditions, and individuals with such combinations of traits are unlikely to arrive at sites with exactly those conditions. The result of this imperfect mapping of fitness traits to niches is that the fitness landscape is relatively broad and flat rather than narrow and sharply peaked, so that achieving equalizing fitness tradeoffs may not be difficult (in contrast to pure neutrality, e.g., Purves and Turnbull 2010), and selective pressure to increase niche separation between species should be reduced.

Our conceptualization of weak neutrality differs from pure neutrality in two key ways. First, rather than specifying that species are exactly equivalent in per capita fitness (Hubbell 1979, 2001), we instead specify that they have broad overlap and are only approximately neutral averaged across spatial and temporal environmental heterogeneity. Broad species overlap rather than per capita equivalence is the equalizing mechanism (Chesson 2000, Adler et al. 2007). This species overlap is similar to other models that consider niche overlap through decreased fitness as species move away from their optimum environment (e.g., Gravel et al. 2006). We expand on this by including two components in this overlap: individual variation in the optimum environment in niche space and decreases in fitness as individuals move away from their optimum environmental conditions. Second, in our formulation of weak neutrality, fixation to a single species is inter-

rupted by stochastic variation in the bias of the random walk. The bias of the random walk is not fixed and constant, but changes with environmental variation in space and time. In pure neutrality, in contrast, speciation is the primary process that prevents fixation of the community to a single species.

Weak neutrality provides a framework that can accommodate dynamics that range from niche-driven to purely neutral depending on the magnitude of species differences, individual variation, and environmental variation. Species dynamics are expected to be predominately driven by weak neutrality when the ratio of intraspecific to environmental variability is high and to be predominantly niche-driven when this ratio is low. Environmental variability also contributes to intraspecific variation through, for example, phenotypic plasticity, and thus we expect phenotypic plasticity to contribute to dynamics that are weakly neutral. Species dynamics in ecological communities may be a mix of neutral and niche processes as the magnitude of individual variability differs across species, the interspecific difference (i.e., bias) varies between species pairs, and environmental heterogeneity fluctuates spatially and temporally (Shmida and Wilson 1985, Gravel et al. 2006, Cadotte 2007). Nevertheless, weak neutrality is likely to be an important and widespread process determining forest dynamics and the diversity of forest trees as well as for other plant and animal communities. We anticipate broad applicability of weak neutrality in community ecology.

Distinguishing between niche and neutral processes using empirical species abundance distributions is problematic (e.g., Chisholm and Pacala 2010), necessitating the need for alternative approaches to distinguish between models of diversity (e.g., Adler et al. 2007). We suggest that experimental studies that examine the validity of the assertions underlying weak neutrality provide one means of examining weak neutrality as a determinant of community dynamics. Experiments are difficult to conduct with long-lived organisms like forest trees, but may be possible with, for example, annual plants or even with microorganisms with short generation times. Empirical studies that, for instance, investigate the relationship between the magnitude of environmental and individual variation and species diversity can be used to examine weak neutrality in communities with long generation times such as forests. Furthermore, the development of analytic or computational models that incorporate the components of weak neutrality can provide for specific predictions of associated species and community dynamics and tests of weak neutrality.

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Erratum - 13 Feb 2012: The original article published on 12 Feb 2012 contained a small number of typographical errors that have been corrected in this version.

