# CONCEPTS & SYNTHESIS

## EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

# The causes of disproportionate non-random mortality among life-cycle stages

Peter T. Green[1] and Kyle E. Harms[2,3]

[1]*Department of Ecology, Environment & Evolution, La Trobe University, Melbourne, Victoria 3086 Australia*
[2]*Department of Biological Sciences, Louisiana State University, Baton Rouge, Louisiana 70803 USA*

*Abstract.* The emergent properties of the collection of species in a natural community, such as diversity and the distribution of relative abundances, are influenced by both niche-based and neutral (stochastic) processes. This pluralistic view of the natural world reconciles theory with empirical observations better than does either a strictly niche- or neutrality-based perspective. Even so, rules (or rules of thumb) that govern the relative contributions that niche-based and stochastic processes make as communities assemble remain only vaguely formulated and incompletely tested. For example, the translation of non-random (non-neutral) ecological processes, which differentially sort among species within a community, into species-compositional patterns may occur more influentially within some demographic subsets of organisms than within others. In other words, the relative contributions of niche vs. neutral processes may vary among age-, size-, or stage-classes. For example, non-random patterns of mortality that occur among seedlings in a rain forest, or among newly settled juveniles in communities of sessile marine communities, could be more influential than non-random mortality during later stages in determining overall community diversity. We propose two alternative, mutually compatible, hypotheses to account for different levels of influence from mortality among life-cycle stages toward producing non-random patterns in organismal communities. The Turnover Model simply posits that those demographic classes characterized by faster rates of turnover contribute greater influence in the short-term as sufficient mortality gives rise to non-random changes to the community, as well as over the longer-term as multiple individuals of a given fast-turnover demographic class transition into later classes compared to each individual that ratchets from a slow-turnover starting class into a later class. The Turnover Model should apply to most communities of organisms. The Niche Model, which posits that niche-based processes are more influential in some demographic classes relative to others, may alternatively or additionally apply to communities. We also propose several alternative mechanisms, especially relevant to forest trees, that could cause dynamics consistent with the Niche Model. These mechanisms depend on differences among demographic classes in the extent of demographic variation that individual organisms experience through their trait values or neighborhood conditions.

*Key words: community assembly; demographics; neutrality; niche; non-random mortality; traits; turnover.*

## Introduction

Hubbell's (2001) Neutral Theory of Biodiversity spurred interest in the extent to which individual organisms within communities (specifically, guilds or same-trophic-level assemblages) are competitively or demographically equivalent across species (e.g., Bell 2001, McGill 2003). Species-compositional dynamics within

an isolated local community of organisms characterized by per capita demographic symmetry (sensu Volkov et al. 2003, 2005) could be especially influenced by ecological drift, analogous to the consequential influence of genetic drift on allelic composition of a small, closed population in the absence of selection (Vellend 2010). Likely owing to Hubbell's use of data from forest dynamics plots to examine the evidence for ecological drift (Hubbell 1979, 2004), multiple data sets from forest plots have been used to test predictions that emerge from neutral theory (Chave 2004). In some cases, observed community-level patterns (e.g., species relative abundance distributions) match expectations strikingly

well (e.g., Rosindell et al. 2011, 2012, Condit et al. 2012).

In contradiction to the symmetry assumption of neutral theory, co-occurring species of trees and shrubs often differ in vital rates, owing to species-specific responses to resource availability (e.g., Dalling and Burslem 2005, Russo et al. 2005), interactions with enemies (e.g., Comita et al. 2010, Mangan et al. 2010), or inherent limits to performance (e.g., Kitajima 1994). In addition, species often differ in key phenotypic traits that interact with the environment to influence individual-level performance under natural conditions (i.e., environmental filtering; e.g., Chase and Leibold 2003, McGill et al. 2006, Paine et al. 2012). The mismatch with neutral theory suggests that species-specific niche differences contribute toward patterning natural forests (Leigh et al. 2004, Leigh 2007). On balance, however, empirical evidence supports a combination of niche-based and neutral mechanisms governing diversity, composition, and dynamics in natural organismal communities (Chave et al. 2002, Wright 2002, Thompson and Townsend 2006, Shipley et al. 2012).

Green et al. (2014) recently examined dynamic patterns of mortality across tree species through the lens of one of the world's longest-running demographic projects, i.e., Joseph H. Connell's censuses of the Davies Creek Forest Dynamics Plot in Far North Queensland, Australia (Connell et al. 1984, 2005). Two key results indicated that both neutral and niche-based processes structure the tree community. First, most mortality in the Davies Creek forest conformed to neutral expectations, in that across all sizes most species died randomly with respect to species identity, i.e., within size classes, the per-stem probability of mortality in any inter-census interval was roughly equivalent among species. The second key result was that non-random processes that manifest in non-random mortality and contribute toward forest assembly and the maintenance of diversity were most influential in the very smallest (and presumably youngest) size classes. Specifically, when cohorts of stems of various sizes were relatively closely matched for sample size and then examined for departures from expectations based on mortality applied at random with respect to species, there were significant departures from random expectation in the smallest, but not the larger size classes. In other words, more non-random structuring occurred in the smaller relative to the larger size classes, a result that supports the ecological intuition of several generations of forest ecologists (Grubb 1977, Harms et al. 2000, Poorter 2007, Umaña et al. 2016).

Below we present two heuristic models that serve as alternative, but not mutually exclusive, hypotheses to account for different degrees of community-level influence from mortality compared among life-cycle stages. We call these hypotheses the "Turnover" and "Niche" Models. Distinguishing between these hypotheses and then identifying their separate and combined contributions toward community assembly would be a significant advance in community ecology, because the former posits that some portions of a community's organisms' life cycles might be especially important structuring stages simply because they are more dynamic, i.e., have faster rates of demographic turnover. In contrast, the latter offers an explanation in which differential niche-based sorting that occurs as organisms pass through key life-cycle classes are more consequential for community assembly than are niche-based processes that operate as organisms pass through other stages.

## Model Components and Assumptions

We develop our two alternative models around a relationship between the proportion of species dying non-randomly and mortality as it culls multiple demographic-class cohorts over time, e.g., individuals of various ages, sizes, or stages followed from an initial census through successively later censuses (Fig. 1). Other formulations could be created to take into account additional or alternative aspects of community assembly, such as spatial patterning across multiple spatial scales, but that is beyond the scope of the current paper.

Consider a single multi-species cohort of individuals of a given size class. Spanning the inter-census interval from the initial census to a later census, a species dies non-randomly if the observed number of individuals that die is significantly different (more or fewer) from the number of deaths expected under Monte Carlo simulations in which the cross-species number of deaths was applied at random with respect to species identity. $P$ is the proportion of species in the size class showing non-random mortality. Cumulative mortality is assessed within the size class as the percentage of stems (of those alive at the initial census) that died across successive census intervals. We argue that a unimodal relationship relating $P$ to cumulative mortality is most likely. If there are very few deaths (especially if the number of deaths is less than the number of species), then few species could experience non-random mortality. In the extreme, if no stems die over a particular inter-census interval, then all species have had 0% mortality, in which case there is no opportunity for inter-specific variation in mortality (i.e., no opportunity for non-randomness, and $P = 0$). Similarly, if most stems die during a particular inter-census interval, then very few species could have died more or less often than expected by chance. In the extreme, if all stems die, then all species have had 100% mortality, in which case there is no opportunity for inter-specific variation in mortality (i.e., no opportunity for non-randomness, and $P = 0$). Maximum non-random mortality probably lies somewhere between these extremes. Each size class has its own relationship relating $P$ to cumulative mortality. For the sake of these arguments we assume that the peak non-random mortality occurs at around 50% and that the curves for each size class are symmetrical between the increasing and declining phases, as depicted in Fig. 1, but the arguments still hold if the curves are skewed in either direction.
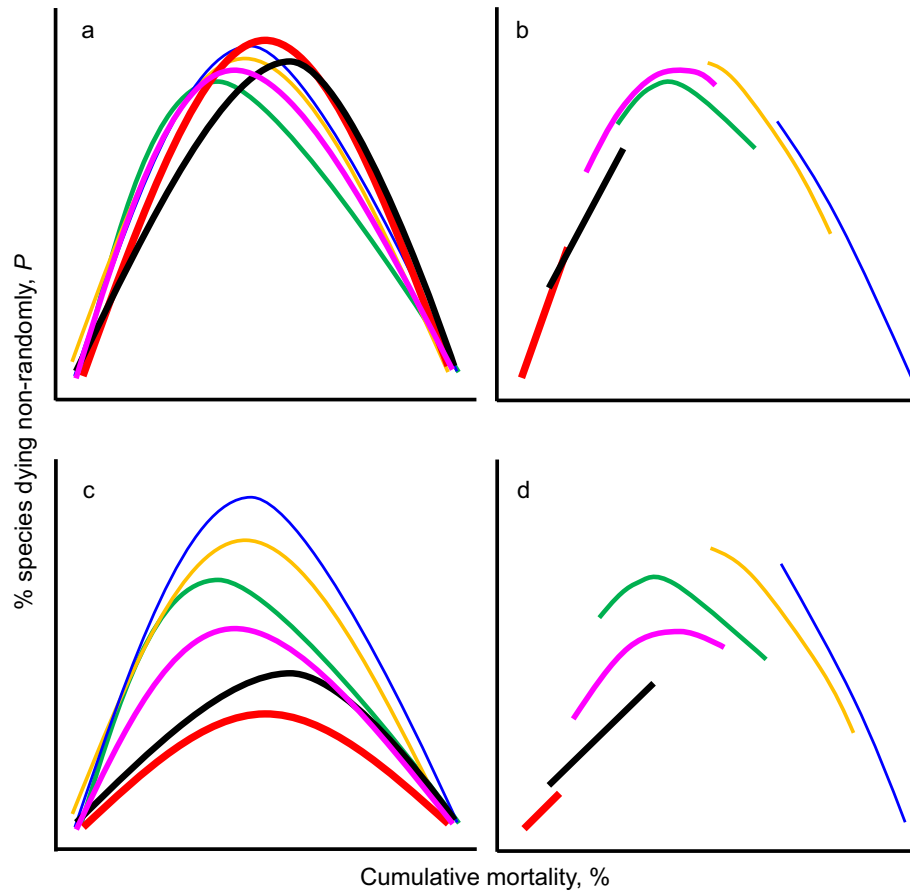
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Fig. 1. Heuristic models that relate the proportion (*P*) of species showing non-random mortality to cumulative stem mortality over undefined periods of time. The minimum and maximum values on the *x*-axis can be thought of as 0% and 100%, respectively. In all models, non-random mortality peaks near 50% stem mortality. (a) In the Turnover Model, peak non-random mortality reaches the same amplitude across all size classes (indicated by different colors, increasing from smallest to largest as blue, orange, green, pink, black, red; the line segments for the size classes increase in width from smallest to largest as well); (b) a given observational study may have sampled only partially overlapping sections of the same common curve. On the other hand, (c) the Niche Model posits that more species will show non-random mortality at most points across the mortality axis in successively smaller size classes, because smaller plants are intrinsically more likely to show non-random mortality than larger plants, for any given level of cumulative mortality. Again, (d) a given observational study may have sampled only partially overlapping sections of the same common curve.

Our models assume that some niche-based differences exist among species. In the absence of niche differences, a community's dynamics would be governed by speciation, immigration, and ecological drift (Vellend 2010). If a community's dynamics were governed by ecological drift alone, the expected curves in Fig. 1 would simply lie flat along the *x*-axis, since species would not be expected to depart from patterns predicted by random mortality. In other words, *P* = 0 throughout the range of cumulative mortality values from 0 to 100%. We do not assume that, in real communities, all species differ from one another (i.e., each species occupies a unique niche), nor that ecological drift is absent. We simply assume that some niche-based differences exist among species and give rise to detectable non-random community structure against the nearly ever-present "noise" of drift.

Neither of our models assumes different average mortality among size classes. If all size classes have the same per capita mortality rate, then for a given inter-census interval (i.e., a given amount of time between censuses) the same total cumulative percentage mortality would have occurred in all size classes.

## TURNOVER MODEL

In the Turnover Model, the proportion of species showing non-random mortality, *P*, peaks at about the same amplitude and at about the same cumulative mortality across all size classes (Fig. 1a). In other words, for a given amount of cumulative mortality the size classes would not differ in degree of non-randomness. Under this model, we are essentially arguing that in a case such as

Green et al. (2014) forest seedlings and large canopy trees are equally likely to show non-random mortality when matched for cumulative amount of mortality, but that we would tend to observe different levels of non-random mortality in the smallest size classes relative to the larger size classes between field censuses, since different amounts of mortality would have accrued among size classes. For example, the community-level differences in non-random mortality observed by Green et al. (2014) would have resulted from sufficient mortality among smaller size classes to reveal non-randomness closer to the maximum, yet insufficient mortality among larger size classes to reveal much non-randomness, even over the 42 years of their study. Under the Turnover Model, we only see sequentially overlapping sections of a common unimodal curve when the size classes are plotted together on a standardized axis (as in Fig. 1b). The mechanism, in this case, for differences among size classes in $P$ at any given point in time since the initial census, is simply different degrees of cumulative mortality having occurred throughout a given inter-census interval. In the specific case of Green et al. (2014), higher average mortality rates occur in earlier life-cycle stages than in later stages, but the general model simply allows for heterogeneity in mortality rates among life-cycle stages, irrespective of which stages differ, or in which particular direction(s).

## Niche Model

The Niche Model (Fig. 1c) offers an intriguing alternative explanation. The general Niche Model posits that the influence of niche-based differences among species changes through ontogeny. In other words, for a matched amount of cumulative mortality, greater non-random mortality would be observed among some life-cycle stages relative to others. In the specific case of Green et al. (2014), greater non-random mortality occurred in the earliest examined life-cycle stage relative to later stages.

There is strong and widespread empirical evidence that organisms vary widely in their susceptibility to processes that cause mortality: the effects of drought, fungal pathogens, herbivores, shading, etc. Most of the empirical evidence for differential susceptibility among forest tree species comes from numerous studies on seedlings (e.g., Comita et al. 2010, Mangan et al. 2010, Bagchi et al. 2014), but differential effects have also been demonstrated for large canopy trees (e.g., cyclones [Curran et al. 2008a, b, Metcalfe et al. 2008], drought [Condit et al. 1995, Newbery and Lingenfelder 2004, 2009], fire [van Nieuwstadt and Shiel 2005], fungal pathogens [Gilbert et al. 1994]). However, if niche-based environmental filtering (abiotic and biotic) is size-dependent and strongest amongst the smallest or youngest individuals, then the proportion of species showing non-random mortality should be highest in the smallest size class and should decline through successively larger size classes (Fig. 1c).

Both Turnover and Niche mechanisms could operate simultaneously. For a given inter-census interval, we expect greater demographic turnover among smaller-sized individuals wherever per capita mortality risks decrease with increasing size. We know of no forest in which this has been investigated, across size classes from tiny seedlings to canopy trees, but in which it is not true (as also indicated in Sarukhán [1978]). Further, we suggest that under both models, non-random outcomes accrue through continuous rounds of recruitment, growth, and mortality, such that the composition of the mature canopy is substantially determined by both faster turnover and more influential niche-derived outcomes in smaller size classes. A variety of niche-based mechanisms could operate in conjunction with and potentially exacerbate the consequences of faster turnover for non-randomness in the smallest size classes.

## Requirements for a Robust Test

A robust test of either model, or of the relative contributions of each, would require enough demographic data to construct the relationship between cumulative percent mortality and $P$ across multiple age-, size-, or stage-classes. The key to distinguish between the models is whether or not the curve relating $P$ to cumulative percent mortality differs among demographic classes. The two hypotheses apply across community types in which individuals recruit from dispersive propagules and then progress through demographic classes. Both models could apply to terrestrial or marine communities, whether the organisms are primarily sessile or are capable of movement from place-to-place throughout their lives.

An experimental test between the Turnover vs. Niche Models could be carried out in a community of short-lived individuals, such as annual plants, by creating a multi-demographic class community. Seeds could be sown for the earliest stage, whereas adult plants could be transplanted for the latest stage. The relative abundances among species could be the same across size classes. In this way, the environmental conditions would be similar across size classes. By following the fates of individuals through time, the stage-specific curves could be produced and compared.

An observational test between the Turnover vs. Niche Models could be conducted by following the fates of individuals through time, beginning with an initial census. The age-, size-, or stage-specific curves could then be compared. In practice, for some types of communities (e.g., forests) even a decades-long observational study may not capture the full range of cumulative mortality for the construction of the curves (Figs. 1b, d, and 2). Consider cohorts of plants alive at the initial census of a forest, each cohort comprising a single size class. Because the annual mortality rate of large trees is extremely low, a decades-long study may yield a cumulative mortality of just 20% or 30%, in which case the observed relationship between $P$ and cumulative mortality would likely be positive. On the other hand, because seedlings have a much higher rate of mortality, a large fraction of
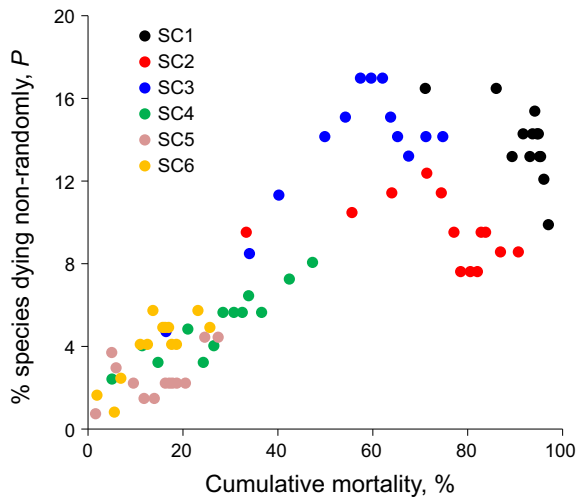
FIG. 2. Empirically derived estimates for the proportion of species dying non-randomly over the 42 years 1971–2013, in six size classes (SC) from tiny seedlings to large canopy trees (redrawn from Green et al. [2014]). For each size class, the points represent a time series from left to right in which a cohort suffered increasing cumulative mortality as the length of the inter-census interval increased. The color key in this figure does not correspond to the colors in Fig. 1.

seedlings may already have died by the first re-census after the initial census, in which case the study may catch just the upper range of the cumulative mortality axis and the observed relationship between $P$ and cumulative mortality could be negative. A hump-shaped relationship would be expected if the observed range of cumulative mortality is in the mid-range. With these real-world considerations in mind, it is likely that in some types of communities (e.g., forests) only overlapping fragments of these curves can be empirically constructed, even after decades of monitoring (Fig. 1b, d).

### EVIDENCE FROM J. H. CONNELL'S DAVIES CREEK FOREST DYNAMICS PLOT

Consistent with the hump-shaped relationships between $P$ and cumulative mortality of both models, we see some empirical support in Green et al. (2014). For example, the shapes of the relationships for two of the three smallest size classes of stems (SC2 and SC3) are consistent with a generally unimodal relationship, spanning both sides of 50% cumulative mortality (Fig. 2). The relationships for the largest size classes (SC4–SC6) follow a generally positive trend, consistent with initial increases in non-random mortality as the cohort dwindles toward 50% cumulative mortality (Fig. 2). The curve for the smallest size class (SC1) is consistent with the declining phase of non-random mortality beyond about 60% cumulative mortality (Fig. 2).

Furthermore, comparisons among size classes indicate that the proportions of species showing non-random mortality tend to be larger in the smaller size classes

relative to larger size classes in which there are common points of comparison in cumulative mortality (consistent with the Niche Model). For example, at 86% cumulative mortality in SC1 16.5% of species died non-randomly, yet only 8.6% died non-randomly in the next larger size class (SC2) for nearly the same cumulative mortality (86.9%). Similarly, 11.3% and 14.2% of species died non-randomly at 40.2% and 49.9% cumulative mortality, respectively, in SC3, but only 8.1% died non-randomly in SC4 at 47.3% cumulative mortality.

Ideally, we would reach a point in our long-term monitoring and data collection on the Davies Creek Plot in which we are able to construct complete curves for each of the size classes, instead of the fragments of curves that we now have (e.g., Fig. 2). We would like to find at least one point of comparison in common to all size classes along the cumulative mortality axis, which would allow us to make an unequivocal evaluation of the hypotheses outlined above. There are two possibilities for doing this. The first is to monitor the smallest size class from an even earlier stage and more frequently, in order to estimate the degree of non-random mortality at a much lower degree of cumulative mortality, commensurate with the lower amount of cumulative mortality already observed for the larger size classes. A second approach would be to continue to monitor mortality in the larger size classes well into the future, until cumulative mortality over many decades in large trees matches the degree of cumulative mortality already observed in the smaller size classes over shorter periods.

### POTENTIAL MECHANISMS UNDERLYING THE NICHE MODEL

There are several hypothetical mechanisms that could cause the key difference between the Turnover and Niche Models, especially as observed in the case study by Green et al. (2014). Each of these mechanisms constitutes a specific ecological process (or set of processes) that could give rise to a dynamic pattern in which niche-based influences would diminish in influence through ontogeny. We describe several of these potential mechanisms below; each is an alternative, non-mutually exclusive hypothesis. We discuss these mechanisms in reference to forests, since our principal observations come from a forest (Green et al. 2014), but they should apply across other community types as well. To elaborate additional mechanisms or to fully evaluate any of them is beyond the scope of the current conceptual paper.

#### Diversity of performance-linked traits

Many traits influence the per capita probability of mortality in plants (Visser et al. 2016). In forests, these commonly include rates of photosynthesis and respiration in relation to light availability, stem wood density, and the mechanical properties of vessel elements, among others (Poorter et al. 2008, Wright et al. 2010). Whereas some traits are likely to be important determinants of mortality across all size classes (e.g., photosynthesis, respiration),

others can only be proximate determinants of mortality in a single size class, such as seed mass and cotyledon form and function for newly germinated seedlings. It is possible that the diversity of traits affecting plant mortality, the total number and the relative importance among the traits, is greatest in very small plants, and diminishes through ontogeny. Although Visser et al. (2016) assessed the relative contributions of four selected traits operating in concert to influence demographic rates among life-cycle stages for trees in a tropical forest, to our knowledge a full assessment across all traits has never been attempted.

### Relative magnitude of trait space

In addition to the diversity of traits per se, the Niche Model would also apply if the range of variation in individual traits among species contracts through ontogeny. The rationale is that if species become more similar to each other for any one performance-linked trait as they grow, then the likelihood of that trait contributing to patterns of non-random mortality should decline through ontogeny. If species become more similar to one another through ontogeny across multiple performance-linked traits, then this contraction of "trait space" (sensu Cornwell et al. 2006) should cause a decline in the proportion of species showing non-random mortality.

Whereas there is widespread evidence that mean values for particular performance-linked traits vary significantly through ontogeny for individual species (e.g., Sterck and Bongers 1998, Martin et al. 2013) and at least one study showed the responsiveness of performance to environmental variables varied through ontogeny (Canham and Murphy 2017), we know of no specific investigations into how trait-space (especially in terms of ranges of values across species for individual traits) varies at the community level through progressive ontogenetic stages (when considering traits measured on individuals of each focal stage-class separately); a larger range in values for key traits among smaller stems could translate into greater among-species differences in demographic performance across environmental conditions. We searched the literature for instances in which performance-linked traits had been measured for small and presumably relatively younger plants, and also larger and presumably much older plants, matched for multiple species at a single site. Data from the La Chonta tropical forest study site in Bolivia support the hypothesis of trait-space contraction (Poorter and Bongers 2006, van Gelder et al. 2006, Markesteijn and Poorter 2009; Fig. 3a). There, specific leaf area spans a 1.7 times greater range of values and exhibits two times greater variance for first-year seedlings compared to larger (presumably older) saplings. Furthermore, stem wood density spans a 1.4 times greater range of values and exhibits 1.6 times greater variance in first-year seedlings compared with saplings. There is also evidence of ontogenetic trait-space contraction in temperate woody trees and shrubs. In the Missouri Ozarks, leaf size spans a 1.8 times greater range of values and exhibits a
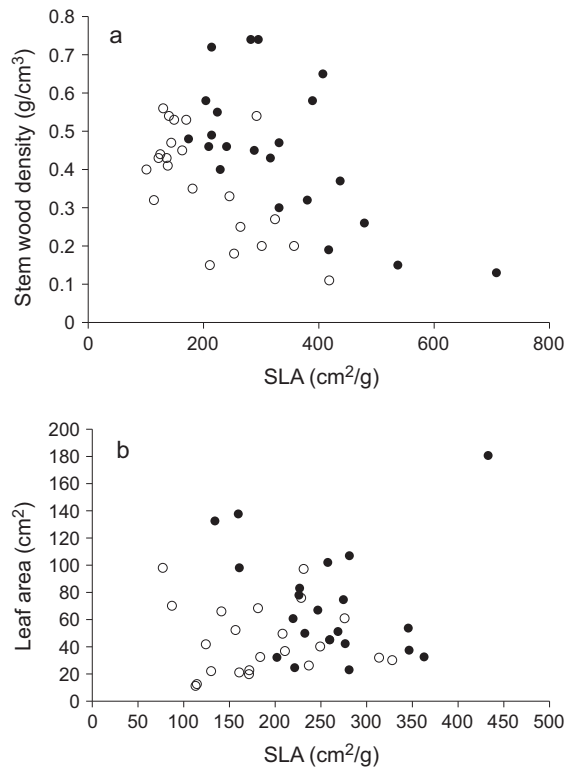


FIG. 3. Ontogenetic variation in trait space for (a) tropical forest and (b) temperate woody species, using published trait values. The tropical forest data come from La Chonta, Bolivia, and compare specific leaf area (SLA) and stem wood density for first-year seedlings (solid symbols) and saplings (open symbols) for 22 species. For seedlings, both SLA and stem density data were extracted from Markesteijn and Poorter (2009). Seedlings were less than one year old, and cross-species mean height was 14 cm. For saplings, SLA data were extracted from Poorter and Bongers (2006) for plants 50–250 cm tall, and stem density data were extracted from van Gelder et al. (2006) for plants 200–400 cm tall. Although collectively these publications report trait data for many more species, only the 22 species for which SLA and stem density data were reported for both seedlings and saplings were included in the figure. The temperate tree data come from the Tyson Research Centre Plot, near St. Louis, Missouri, USA (Spasojevic et al. 2014), and compare leaf size and SLA for saplings (solid symbols) and adults (open symbols). Saplings were defined as <10-cm dbh for tree species, and <5 cm dbh for shrub species. Larger stems were considered as adults. Only those species with $n \geq 5$ stems were included in the figure.

2.6 times greater variance for saplings vs. adult stems, but neither the range nor cross-species variance in SLA differs between saplings and adults for a matched set of 22 species (Spasojevic et al. 2014; Fig. 3b).

### Relative variation in neighborhood composition and attack by enemies

Neighborhoods matter, often such that better performance is linked with both increased diversity and decreased phylogenetic relatedness of focal plants to their neighbors (Webb and Peart 1999, Peters 2003, Metz et al.

2010, Bagchi et al. 2014, Wills et al. 2016). The Niche Model would apply if the range of neighborhood species-compositional variation were greater for smaller individuals relative to larger individuals, in terms of cohort neighbors of similar-sized individuals. That is, seedlings and small saplings might have a greater range in neighborhood variation than large trees. The especially relevant neighborhood variation might be the proportion of near-neighbors that are conspecifics (or congenerics or confamilials; see Gilbert and Webb 2007). If enemies (i.e., animals or microbes that consume biomass) cue into density or frequency, then neighborhood relatedness influences probability of mortality owing to those enemies. If the proportion of near-neighbors that are conspecifics (or otherwise relatively closely related) ranges across a broader set of values for smaller saplings than larger trees (as seems likely, since conspecific seedling carpets are common, but conspecific groves of big trees are not), then the overall range of neighborhood conditions varies more for smaller plants than larger.

We tested the prediction that neighborhoods of smaller individuals cover a broader range of variation than neighborhoods of larger trees with data from the Davies Creek Plot. To match the size classes used in Green et al. (2014), we used the stems that were alive on the plot in 1971 and compared the smallest size class (SC1 and SC2 combined) to the largest size class (SC6). The smallest size class comprised all stems ≤15.2 cm height mapped within transects that cross the Davies Creek Plot (transect details can be found in Connell et al. 1984, Connell and Green 2000). The largest size class comprised all trees ≥10 cm diameter at breast height throughout the 1.7-ha plot. For each individual in each of the two size classes we found the 10 nearest neighbor individuals in the same size class. To avoid edge effects (i.e., focal stems whose neighborhoods were not fully contained within censused areas), we then selected those individuals that were nearer their closest 10 neighbors than to a transect edge (for the smallest stems) or to a plot border (for the largest trees). For the smallest stems, we had 728 focal individuals whose 10 nearest same-size-class neighbors were mapped and identified; for the largest trees we had 1,050. The number of conspecific neighbors within a focal stem's nearest 10 neighbors averaged 4.1 and ranged from 0 to 10 for the smallest stems, but averaged 0.5 and ranged from 0 to 6 for the largest trees. The number of species among a focal stem's nearest 10 neighbors averaged 4.0 and ranged from 1 to 10 for the smallest stems, but averaged 8.3 and ranged from 4 to 10 for the largest trees. In this example, local neighborhoods of similar-sized stems covered a broader range of values for the smallest stems as compared to the largest trees, based both on proportion of neighbors that were conspecifics and on neighborhood species richness.

### Relative hazard load

On average, the youngest or smallest individuals may face a greater diversity of potentially lethal hazards than later-stage organisms. Once again, we do not know this to be true, nor to our knowledge has it been tested, but we articulate this as an additional mechanistic hypothesis. It may be that most hazards disproportionately affect some size classes. For example, damage from falling litter, trampling, and overland flow during torrential rains are hazards that primarily directly impact seedlings in a forest (e.g., Clark and Clark 1989, Theimer and Gehring 1999), whereas lightning strikes essentially only directly affect large trees (Yanoviak et al. 2015), and drought may be more consequential to larger than smaller trees (Bennett et al. 2015; although an assessment across the full range of life-cycle stages has not, to our knowledge, been attempted). It may be that the set of hazards is larger for smaller relative to larger individuals.

Regarding enemies of host plants, there may be more species-specific enemies of smaller sized individuals than larger sized individuals. This could occur if there is more enemy-sharing among larger sized individuals. Consequently, the variation in enemy-related mortality should be greater for smaller sized plants, since each species-specific enemy may have its own characteristic level or type of average damage. This could be true if as trees progress through development they accrue more-and-more or better-and-better defenses (which links back to traits). Surveys of the richness of damage types among species (e.g., Bachelot and Kobe 2013), and of the agents causing the damage, would need to be conducted across ontogeny to assess this idea, but we are not aware that any studies of this kind have been completed.

### Relative impact of damage from enemies

Traits and neighborhoods are two niche-based factors that create non-random outcomes in plant performance, and both can affect the per capita probability of mortality by determining in part the amount of damage experienced by plants (e.g., Coley 1987, Bachelot et al. 2015). One of the reasons that plants die is because they get damaged beyond the point from which they can replace tissue lost to enemies. In a community of individuals there is likely some positive relationship between the amount of damage and the probability of mortality. We suggest that size-based differences in maximum likely amounts of damage to living tissue, and the effect of that on per capita probability of mortality, could be a significant niche-based mechanism underlying the greater propensity of smaller plants to show non-random mortality.

For the sake of simplicity, we represent the relationship between the amount of damage and the per capita probability of mortality as a linear one (Fig. 4). For seedlings, empirical observations indicate that even though some seedlings persist virtually unscathed in the understory, others may be consumed totally (e.g., Coley and Barone 1996). Thus, the range of damage (x-axis) across individual seedlings is from near 0% to 100%. The impact of this damage on per capita probability of mortality is also
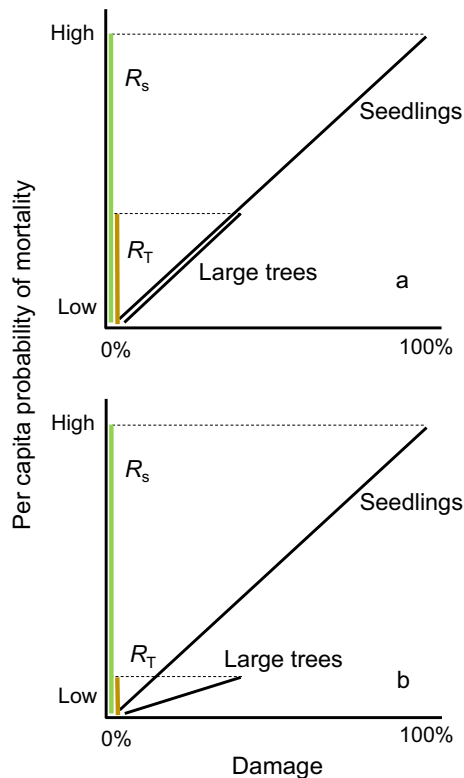
FIG. 4. Hypothesized relationships for ontogenetic variation between the amount of damage inflicted by natural enemies and per capita probability of mortality, in which (a) the two size classes share a common slope and intercept, and (b) where large trees have a shallower slope but the same intercept, which we think is more likely. In both models $R_S$ is the range of per capita probabilities over the full range of damage likely experienced by seedlings (indicated by the vertical green line along the $y$-axis), and $R_T$ is the range of per capita probabilities over the full range of damage likely experienced by large trees (indicated by the vertical brown line along the $y$-axis).

similarly broad, again for the sake of simplicity, we indicate this as low to high on the $y$-axis (we note that 100% removal of leaves and stems of the newly germinated seedlings of species with epigeal cotyledons will result in a 100% probability of mortality, but this will be less than 100% for species with hypogeal germination because of their capacity to resprout; Harms and Dalling 1997, Green and Juniper 2004$a$, $b$). On the other hand, large trees may more rarely suffer life-threatening damage from enemies, and in our illustration we have arbitrarily set the maximum to about 30%, noting that our arguments below work equally well for larger amounts, and even better for smaller amounts. The impact of this amount of damage on the probability of mortality is probably very low. Accordingly, the relationships for both seedlings and large trees share the same slope and intercept (Fig. 4a). However, the range in per capita seedling mortality would be much greater than that for large trees, simply because seedlings can suffer a greater range of damage in the proportion of photosynthetic tissue lost to enemies.

So far under this mechanism, the per capita probability of mortality is the same for seedlings and large trees, within the common range of observed damage. This is unlikely to be true, because for the same amount and type of damage, seedlings are probably at greater risk of mortality because they mostly exist close to the compensation point in shaded understories, with limited capacity to achieve net positive growth if they suffer tissue damage or loss. We think a more realistic version of these relationships would portray the slope of the relationship between amount of damage and per capita probability of mortality as shallower for large trees than it is for seedlings (Fig. 4b). This would have the effect of narrowing even further the range in per capita tree mortality over the observed range of damage, and exacerbating the difference in the ranges between seedlings and large trees.

In both versions of the mechanism, the demographic outcomes of damage are more similar across species for large trees than for seedlings; that is, mean species mortality is more variable among seedlings than large trees. These differences could give rise to greater non-random mortality in smaller than larger size classes. These mechanisms could be further refined by consideration of non-linear, threshold effects, and could be broadened to include other types of hazards, such as drought and shade.

## IMPLICATIONS FOR UNDERSTANDING COMMUNITY DYNAMICS AND FOR MANAGING COMMUNITIES

We were motivated to construct our two alternative models based on empirical observations from a forest dynamics research plot. Therefore, the models are especially relevant to plant communities that regenerate primarily from seeds, but they should apply to most other types of communities as well, especially those dominated by sessile organisms with dispersive propagules.

In general support of our basic premise, several recent assessments of stage-specific influences on plant community assembly have found that non-random processes have more influence early during the life cycle than do non-random processes operating in later stages. Zhu et al. (2015) directly compared seedling, sapling, juvenile, and adult stages among 29 species in the rain forest tree community on Barro Colorado Island (BCI), Panama. They used generalized linear mixed-effects models to characterize focal individual survival as a function of conspecific neighbor density, as well as heterospecific neighbor density and phylogenetic relatedness, and found a decline in the strength of conspecific negative density dependence from seedlings through later life-cycle stages. Chu and Adler (2015) directly compared the recruitment stage to later stages in grassland and shrubland communities in North America via empirically informed population modeling, and found that the processes operating during early life-cycle stages created especially influential niche-based stabilizing effects. Velázquez et al. (2016) made an indirect comparison of their own spatial point pattern analysis of the 1–4 cm diameter at breast height sapling stage in the

rain forest on BCI to previously published studies of seedlings and smaller saplings in the same community, and concluded that conspecific density-dependent mortality was relatively unimportant among saplings relative to earlier studies on seedlings and smaller saplings. From this set of studies, it is clear that a variety of methods could be brought to bear on the comparative question of how different life-cycle stages influence community-level changes through mortality or other demographic processes.

We expect the Turnover Model to apply in all horizontal communities (i.e., species of a given trophic level occupying a given place at a given time; sensu Vellend 2016). If there is any non-neutrality, i.e., niche-based mechanisms that to a degree bias demographic success and failure among species, then more dynamic demographic classes (those with greater turnover) should be especially influential to overall community dynamics. If the contributions of non-neutrality also vary among demographic classes when matched for levels of mortality, then one or more mechanism(s) underlying the Niche Model should also apply. Since deterministic niche-assembly mechanisms are necessarily the processes that would give rise to any observed non-random patterning in any of the demographic classes, both models are consistent with all types of coexistence mechanisms (sensu Chesson 2000) and all types of local extinction mechanisms, such as competitive exclusion (Hardin 1960), that could produce non-random patterns. The distinguishing feature between the two models is whether (Niche Model) or not (Turnover Model) those deterministic mechanisms operate more consequentially in one or some demographic classes relative to the others.

To understand the non-random contributions to community composition caused by differences in mortality rates among demographic classes (Turnover Model) and those further caused by ontogenetic differences for matched mortality (Niche Model) could also improve management and restoration of communities. Just as identifying critical life-cycle stages in population dynamics allows managers to target the most relevant processes impacting population viability (e.g., Morris and Doak 2002, Raghu et al. 2006), so too would understanding the most critical influences on community dynamics.

For relevant natural and managed communities, we envision a future exercise in which one would model community dynamics (possibly most usefully via individual-based simulation) to evaluate the extent to which different age, size, or stage classes influence overall dynamics and composition. We have made our arguments based on comparisons of mortality among demographic classes, so an open question remains regarding the influences these differences have on overall community dynamics and composition. We postulate that, under most circumstances, the class(es) with greater demographic turnover (higher mortality and recruitment rates) should be especially influential to overall community dynamics. Those individuals in each demographic class that survive and transition into the next demographic class will carry with

them any non-random outcomes accrued while they occupied the immediately preceding demographic class. For a given period of time, more individuals ratchet out of the demographic classes with higher turnover, such that the contributions of those demographic classes should compound through time. Even so, the complexity of community dynamics that emerge from the dispersal, recruitment, development and growth, reproduction, and mortality of its component individuals could obscure or override the influences of mortality processes alone. A community-dynamics model could evaluate the relative contributions among all demographic classes (from dispersive propagules to the oldest individuals) toward non-random community-level temporal or spatial patterning contributed via the Turnover or Niche Models, or both relative to ecological drift.

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