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Spatial Variation in Tree Community Assembly

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Spatial Variation in Tree Community Assembly

by

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Dedicated to my family, who have always encouraged me

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Spatial Variation in Tree Community Assembly

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Spatial variation in tree community composition and assembly is due in large part to dispersal limitation, spatial variation in environmental conditions, and interactions among competing trees. The relative importance of these processes may be governed by landscape structure and environmental conditions. (I) The movement of frugivores between remnant forests and successional areas is vital for tropical forest tree species to colonize successional habitats. I found that avian frugivores crossing forest edges were generally insensitive to percent cover and clustering of pasture trees. If pastures were abandoned the distance from forest edges would not likely limit frugivore visitation and seed deposition under pasture trees in my study. (II) Relatively little is known from a theoretical conservation perspective about how reserve size affects communities assembled by abiotic and dispersal limitations. Simulated small reserve systems increased the distance between environments dominated by different species, diminishing the importance of source-sink dynamics. I found a trade-off between preserving different aspects of natural communities, with greater α-diversity in large reserves and greater γ-

diversity across small reserve systems. (III) Functional trait diversity of co-occurring organisms may be indicative of the processes that structure communities. Across spatial scales, an axis of leaf succulence exhibited the strongest evidence for niche-based assembly among co-occurring *Ficus* individuals, whereas specific leaf area (SLA) showed the strongest evidence for niche-based assembly among species. Trait analyses of co-occurring individuals had greater power than analyses at the species level, especially for traits with high intraspecific variation. Environmental filtering may be stronger at higher elevations due to drought stress. (IV) Individual fitness is a function of the interaction between traits and environment, or environmental selection. I estimated spatial selective gradients affecting a subtropical tree community and found that the trait axes with the strongest selection were also those with the least spatial variation. Interestingly, factors associated with selection were quite different for growth versus survivorship. The trait-by-environment interactions I identified are strong candidates for spatial niche differentiation, and may explain how tree species coexist in this diverse subtropical forest.

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Chapter I

The Effect of Spatial Structure of Pasture Tree Cover on Avian Frugivores in Eastern Amazonia

INTRODUCTION

Secondary forests will dominate many future tropical landscapes, but it is unclear if and how quickly they will return to pre-deforestation composition (Wright & Muller-Landau 2006). The movement of frugivores between remnant forests and successional areas is vital for tropical forest tree species to re-colonize secondary habitats (Nepstad *et al*. 1996, Harvey 2000, Hooper *et al.* 2005). The spatial structure of a landscape, meaning the composition and configuration of environmental conditions across an area (as opposed to at a point), can generate non-random patterns of animal movements and distribution (McIntyre & Wiens 1999, Levey *et al.* 2005). Isolated patches of tree cover in human-dominated landscapes are used by many native animal species and can be important in maintaining animal diversity (Hughes *et al.* 2002, Harvey *et al*. 2006, Manning *et al.* 2006). Little is known, however, about how the spatial structure of pasture tree cover affects the movements of frugivores.

Animals moving across patchy landscapes face many boundary-crossing decisions, which affect their spatial distributions (Turchin 1991, McIntyre & Wiens 1999). Animals

move limited distances in order to locate appropriate foraging substrate (Fitzpatrick 1980, Robinson & Holmes 1982), and can prefer locations where foraging substrate is clustered (Edwards *et al.* 1994). Species inhabiting edges often move limited distances away from edges in either habitat (da Silva *et al.* 1996, Laurance *et al.* 2004) and cross gaps of limited size (Lees & Peres 2009). Edge and forest species may avoid large open habitats because of increased vulnerability to predation (Rodriguez *et al.* 2001).

Frugivores that visit pastures often frequent pasture trees and avoid the large expanses of pasture that are common in eastern Amazonia (da Silva *et al.* 1996, Estrada *et al.* 1997, Sekercioglu *et al.* 2007). Pasture trees receive high seed deposition relative to the rest of pastures, have an ameliorated microclimate (Belsky & Canham 1994, Vieira *et al.* 1994), and generate nuclei of woody successional growth (Guevara & Laborde 1993, Nepstad *et al.* 1996). Non-fruiting pasture trees may attract as much outside seed rain as fruiting trees and are important facilitators of succession (Carriere *et al.* 2002a, Zahawi & Augspurger 2006). I focus on studying frugivore visitation to non-fruiting trees, avoiding variation in crop size that could obscure spatial effects (Howe & De Steven 1979).

Existing literature has largely overlooked the effects of the percent cover and configuration of pasture trees in promoting visitation by tropical frugivores. Researchers have examined how frugivore visitation to pasture trees changes over distance from forests edges (da Silva *et al.* 1996, Luck & Daily 2003, Eshiamwata *et al.* 2006, Zahawi & Augspurger 2006, Berens *et al.* 2008). The results from these studies are conflicting, possibly because researchers did not consider the explicit spatial arrangement or percent

cover of pasture trees in the landscape. In studies of frugivores that included data on locations of pasture trees, the effects of spatial distribution of pasture tree cover were not explicitly analyzed (Graham 2001, Sekercioglu *et al.* 2007). Higher clustering of pasture trees (i.e. shorter average distance between trees) may promote visitation because many species move limited distances across pasture between trees (da Silva *et al*. 1996).

The frugivorous birds that most frequently cross forest pasture edges are typically facultative, non-specialist frugivores, while specialist frugivores tend to be less likely to cross from forest into pasture (da Silva *et al.* 1996, Lindell *et al*. 2004, Zahawi & Augspurger 2006). As a result facultative frugivores common to forest-pasture edges play an important role in dispersing seeds from forests into pastures merely due to the frequency with which they cross forest edges (Guevara & Laborde 1993). Facultative frugivores might also be more likely to visit and deposit seeds at non-fruiting trees than specialist frugivores. My study species were largely facultative frugivores (species of low and medium frugivory in Table 1.1).

I determined how visitation of avian frugivores to pasture trees is correlated to small-scale tree cover structure in eastern Amazonia at the edge of primary forest fragments and extensive pastures. I focused on five variables of frugivore visitation that may be positively correlated to the intensity and diversity of local seed deposition: (1) frugivore presence, (2) frequency of frugivore visits, (3) duration of visit (Schupp 1993), (4) species richness of frugivores, and (5) an index weighting frugivore visits by their seed dispersal potential. I studied the relationship between the five response variables and four measures of the spatial context of pasture trees and tree size: (1) percent pasture

tree cover, (2) clustering of pasture tree patches, (3) distance between tree and primary forest edge, and (4) tree crown area. A fifth covariate, tree height, was measured but not included in analyses because it was strongly correlated with crown area.

I predicted that some study species of avian frugivores would prefer forest edge habitat and respond negatively as pasture tree cover became more sparse and isolated. I expected that for those sensitive species, response variables would exhibit three patterns: (1) positive correlation to increasing pasture tree cover, (2) positive correlation to more clumped tree distribution, and (3) negative correlation to distance to forest edges. I predicted that my index would show stronger responses to spatial structure than raw frugivore counts, because I expected species with the highest potential to disperse forest seeds (i.e. highly frugivorous forest species) to be more sensitive to structure. Finally, I expected more and longer visitation to larger trees, which presumably contain more resources.

METHODS

Study site

The study site was the Fazenda São Marcos (2˚11’54” S, 47˚20’58” W). The site is a ranch located at an elevation of 90 m asl in the Capitão Poço municipality of the state of Pará, Brazil, in eastern Amazonia. Rainfall at the site is ~2000-2500 mm yr^{-1} (Oliveira *et al*. 2002), with a dry season lasting on average from June to November (Uhl *et al.* 1988). Soil at the study site is yellow latosol (SIPAM 2006). Sampling occurred along the edges

of two evergreen, terra firme primary forest fragments (3800 and 900 ha) that were surrounded by actively grazed pastures. Successional habitats in the region are described in detail by Uhl *et al.* (1988). Fazenda São Marcos pastures extended at least 500 m from the forest edge. Narrow (<20 m) strips of riparian tree cover were present at sites and were included in tree cover surveys. The study was conducted throughout October-December 2007, in the late dry season. Although fruiting of woody species is greater in the rainy season, about one third of frugivore individuals in pastures had seeds of woody species in their feces during the dry season, indicating a significant potential for dispersal even in the dry season (da Silva et al. 1996).

Tree cover surveys

Sampling was conducted at 20 forest edge sites with ~1 km between each site. For use in subsequent bird surveys, three non-fruiting focal trees in the pasture were selected at each site. Focal trees did not have fruiting epiphytes during the study. Trees were selected to capture variation in distance to forest edge within plots at each site. Trees were a mix of remnants pre-dating deforestation (ca. 1975) and younger pioneers. Trees were not completely identified as part of this study. At each site, a semicircular plot was formed in order to measure spatial structure of tree cover in the local landscape (Figure 1.1). The center point of each of the 20 plots was located using the following method. Using a GPS unit (Brunton MNS, typically less than 15 m RMS error), three edge points were located where a line from each focal tree met the forest edge perpendicularly. The mean of the three edge points was then taken as the center of a semicircle.

The plots were created with a radius of 200 m, resulting in semicircles of ~ 6.5 ha, centered at the forest edge. The selection of a 200 m radius allowed us to encompass the distance of most movements of study species, based on published results for three of my study tanager species (da Silva et al. 1996) and on my personal observations. da Silva et al. (1996) found that the three species' incursions reached 60 m into pastures on average, with an average species maximum distance of 179 m. Expanding the size of plots beyond 6.5 ha was limited by the time and resources available to conduct detailed mapping of tree cover.

In each plot, all pasture trees of height ≥ 2 m were mapped with a GPS unit and had two perpendicular diameters of their crown measured. Calculations of tree crown area assumed elliptical shapes. The height of trees was determined using a clinometer. The boundaries of continuous canopy patches of pasture trees were recorded with GPS.

I calculated three spatial metrics potentially important to frugivore visitation: (1) “cover” as the percentage of the 200 m radius pasture plot covered by tree canopy, (2) “clustering” as the average nearest neighbor (ANN) index of the plot, and (3) distance from each focal pasture tree to the forest edge. The ANN index is computed by dividing the observed mean nearest neighbor distance between tree patch centroids by the expected distance based on random placement (expected = $0.5/(n/A)^{1/2}$, where n is the number of patches and A is the area surveyed). Calculations were done with ARCGIS v. 9.2 (ESRI).

Avian frugivore surveys

I assumed that avian frugivores found in the forest were potential dispersers of forest seeds. I estimated species abundances in the forest edge in order to assess species potential to serve as vectors of primary forest tree seeds. I conducted point counts of frugivores in the forest edge. One 10 min point count was conducted at each site, occurring between sunrise and 3 h 15 min later. Point counts were based at the center point of each of the 20 semicircular plots, which were at the forest edge. Only birds located in the forest were recorded. The distance to each individual detected within 100 m was estimated to model the decay in detection probability with distance (Buckland *et al.* 2001). Distances were divided into four 25 m-wide bins.

Abundances were estimated with the distance-sampling model of Royle *et al.* (2004) that considers local counts as a Poisson or negative binomial-distributed random variable. The Poisson model has two parameters, θ, which is the standard deviation of the half-Gaussian function used to represent detection probability versus distance, and λ, the mean abundance. The negative binomial model includes a third parameter k, describing the over-dispersion of the count data (Royle *et al*. 2004). Parameter values for the Poisson and negative binomial models of abundances were estimated using maximum-likelihood, calculated in R (R Development Core Team 2008). Poisson and negative binomial models were compared via Akaike's information criterion (AIC). Each species' abundance in the forest edge was taken as the maximum-likelihood estimator of the abundance parameter λ from the AIC-selected model. Uncommon species had ill-conditioned likelihood functions, making it impractical to estimate all parameters of the abundance model for each uncommon species. Estimates of θ from models of single,

common species did not vary widely (C.V. = 0.17), thus I estimated a single detection parameter θ for all uncommon species. I then used this estimated θ in the abundance model and found the maximum-likelihood estimator for each species abundance λ.

Each of the three non-fruiting pasture focal trees at each sampling site (N = 55 trees, 5 were excluded after they began fruiting) were observed for a 30 min period from sunrise to 3 h 15 min later, the peak period of bird activity. During each 30 min observation period the time of entry and exit and species identity of each bird landing on the tree was recorded from a distance of ~ 50 m away, using 8.5 X 44 binoculars. I was positioned so as to obscure myself in pasture vegetation, and birds in the vicinity of the focal tree did not visibly respond to my presence. Sallying flights to catch aerial insects or to glean insects from the focal tree were not recorded as exits if the bird returned. I only included duration of visit observations if both the entry and exit of the bird were observed. The mean species' duration of visit to a single focal tree was used as an individual observation in statistical analyses. The observations at the focal trees at each of the 20 sites were conducted across at least two different days for each site.

I modeled visitation (i.e. presence, visitation rate, and duration of visit) of individual frugivore species and the aggregated visitation of frugivore species. Species were considered frugivores based on reports in the literature (Moojen *et al*. 1941, Morton 1977, Fitzpatrick 1980, Karr *et al.* 1990, Poulin *et al*. 1994, Arteaga *et al*. 2006, da Mota Gomes *et al.* 2008). I aggregated species in several ways, based on taxonomy, level of frugivory, and abundance in pasture trees, in order to determine if groups showed distinct relationships to spatial structure. At the broadest level, I aggregated visitation of all

frugivore species for analysis. I also aggregated into two separate groups the visitation of Tyrannidae and Thraupidae species, the two most important families of pasture-edge frugivores in the region (da Silva *et al.* 1996). In addition, I aggregated movements of species of similar levels of frugivory. I reviewed available literature and divided species into three groups of 1) low (i.e. species where <10% of individuals had fruit in gut), 2) medium, and 3) high frugivory (i.e. where >80% of individuals had fruit in gut) based on diet data (see previously cited references; Table 1.1). I aggregated visitation of frugivores uncommon in pastures, in order to determine if relatively rare species showed distinct patterns (Summerville & Crist 2001, Lasky & Keitt 2010). This group consisted of species detected five or fewer times in pasture trees (too few to model their species-specific movement) and is referred to below as the "group of uncommon frugivores."

I computed an index to estimate differences among pasture trees in expected seed dispersal from forest sources. The index is a modified version of an index that estimated the importance of dispersers based on abundance and level of frugivory (Galindo-González *et al.* 2000, Arteaga *et al.* 2006). The index was calculated for each species at each pasture tree as the product of three quantities: 1) number of visits, 2) species abundance in the forest edge (as estimated from the above described 100 m radius point counts), and 3) the rank of the species level of frugivory. The index was then summed across all species observed at each tree. I refer to this as the forest-frugivory index. Species of low frugivory received a rank value of 1, species of medium frugivory received a 2, and species of high frugivory received a 3. The results I report below were qualitatively consistent and nearly identical using a wide range of rank values for the 3

level of frugivory groups (an example of an alternative quantification of ranks giving similar results: low frugivory = 1, medium frugivory = 2, high frugivory = 5).

Modeling frugivore visitation

The three response variables of frugivore visitation (i.e. presence, visitation rate, and duration of visit) were analyzed with hierarchical linear mixed-models. Models took the general form:

$$g\left(E\left(Y_{ij}\right)\right)=\beta_0+\beta_1 x_i+\gamma_{0j}+\gamma_1 w_j \qquad (1)$$

and

$$\gamma_0 \sim N\left(0,\sigma^2\right) \quad (2)$$

where the expected value of an observation ($E(Y_{ij})$) in tree *i* in plot *j* is related to a linear model via the appropriate link function, *g*. The model includes vectors of covariate parameters ($\boldsymbol{\beta_1}$ and $\boldsymbol{\gamma_1}$, respectively) for the effects of conditions at the level of the sample tree ($\boldsymbol{x}_i$) and at the level of the plot ($\boldsymbol{w}_j$). In addition to the fixed-effect general intercept term, β_0, there is a normally distributed random variable for each plot intercept, γ_{0j}. The plot intercept term was included because the errors of each set of three pasture trees in the same sampling plot might not be independent.

I modeled the effects of two plot-level covariates ($\boldsymbol{\beta_1}$) of spatial structure: percent pasture canopy cover and ANN index, and two tree-level covariates ($\boldsymbol{\gamma_1}$): distance from tree to forest edge and crown area of the pasture tree. Distance and crown area were log transformed while canopy cover was logit transformed in order to generate

approximately normally distributed covariates. All covariates were scaled to have mean zero and unit standard deviation.

I modeled the effect of the covariates on five response variables of bird visitation: (1) presence of bird in focal tree, (2) number of visits to focal tree, (3) duration of visit to focal tree, species richness in the focal tree, and (5) the forest-frugivory index. I modeled presence in addition to visitation rate because I wanted to model a variable independent of rapid repeated visits by the same bird. Presence was modeled as a Bernoulli response with the logistic link function. The number of visits and species richness were modeled as a negative binomial response with a log link function, appropriate for count data where observations are over-dispersed and non-independent. Duration of bird visits were modeled as the mean of a beta distribution, which is appropriate for responses that are restricted to an interval (duration was limited by 30 min observation periods). In this regression, I used a recently developed link function that allows one to model the mean of the beta distribution, a technique yet to be used extensively in ecology (Ferrari & Cribari-Neto 2004). Finally I modeled the forest-frugivory index using a two-part model, because the data followed a zero-inflated log-normal distribution. I used the two-part regression model of Li *et al*. (2008), with a slight modification suggested by Su *et al*. (2009). The model combines a logistic function modeling presence with a log-normal function modeling the forest-frugivory index, where covariate terms are included in both functions and plot-level error terms are correlated between functions. I also used the two-part model to estimate covariate effects on the number of visits of all frugivores, in order to compare parameter estimates from the same model when considering raw count data

of number of visits vs. the forest-frugivory index.

I used hierarchical Bayesian inference to estimate the values of model parameters. I attempted maximum likelihood techniques but resulting parameter estimates were unrealistic. Hierarchical Bayes methods allow complex multi-level models (e.g. tree level and patch level effects) to be decomposed into smaller problems (Clark 2005). Sampling methods of Bayesian inference (e.g. Gibbs sampler) use the likelihood of the data and the prior probability of the parameters to sample from the posterior probability distribution of parameters, defined as the probability of parameter values given the observed data. Here, I report 95% credible intervals (CI) of covariate effects $\boldsymbol{\beta_1}$ and $\boldsymbol{\gamma_1}$, which mean that there is a 95% probability that the true parameter value lies within the interval, given the data. I highlight covariate effects where their 95% CI does not include zero, but I also note some covariates where effects have more marginal support. I note this range of results in order to avoid simple null hypothesis testing, which can be relatively uninformative and oversimplify results (Anderson *et al.* 2000).

I estimated Bayesian posterior distributions of model parameters using a Gibbs sampler to generate Markov Chain Monte Carlo (MCMC) samples. Sampling was conducted using the JAGS 1.0.3 (http://calvin.iarc.fr/~martyn/software/jags/) software. Parameters were given diffuse priors ($N(0,100)$ for the slopes of all covariates $\boldsymbol{\beta_1}$ and $\boldsymbol{\gamma_1}$). Convergence of posterior MCMC samples was verified for all models through inspection of trace plots.

Sampling of posterior probability distributions failed to converge for species with few detections (although species with five or fewer detections in pasture trees were

modeled in aggregate as the 'uncommon frugivores'). I restricted modeling of each response variable to species that were 1) recorded in at least six focal trees (for presence models), 2) with at least nine visits (for visitation models), or 3) with visits of known duration for at least eleven sample trees (for duration of visit models).

RESULTS

Tree cover surveys

I mapped cover of all pasture trees at least 2 m tall across a total of 129.6 ha of pasture at the 20 sample sites, with each plot covering a mean of 6.5 ha (range = 5.7, 7.6; SD=0.4). Mean canopy coverage in plots was 5.4 percent (range = 0.1, 31.2; SD=8.1). Plots had a mean ANN index of 0.9 (range = 0.4, 1.4; SD = 0.3). The 55 focal pasture trees were on average 10.8 m tall (range = 5.0, 22.7; SD=3.6) with a crown area of 62.6 m^2 (range = 3.8, 296.6; SD=56.0). The mean distance between focal pasture trees and the primary forest edge was 84.6 m (range = 1.6, 183.8; SD=58.6).

The two spatial structure covariates, tree cover and ANN index, were independent (ANOVA, $p = 0.68$, $R^2 = 0.01$), which was expected because ANN corrects for the number of trees. Focal tree height and crown area were strongly correlated (Spearman's $\rho = 0.54$), while the other covariates were not significantly correlated (data not shown). Crown area was independently a better predictor of frugivore responses than tree height was, thus I included only crown area in models.

Bird surveys

The twenty forest edge point counts yielded 101 individuals of 16 species of frugivores that I also observed in pasture trees. These species can potentially transport seeds from forest to pasture. The most abundant frugivore in the forest counts that also visited pastures was *Ramphocelus carbo* (Table 1.1). Poisson abundance models were selected for five species, while over-dispersed, negative binomial abundance models were selected for five species. Six uncommon species were detected too infrequently to model species-specific detection decay parameters. A single detection parameter was estimated for the aggregated data of these species, and a Poisson abundance model was selected for them.

In focal observations of 55 pasture trees, I detected 21 species of avian frugivores that occur within primary forest edges (Ridgely & Tudor 1989; Table 1.1). These species had 197 visits to pasture trees during surveys. Both the birds' entrance and exit were observed for 124 visits (observations used to model duration). *Thraupis episcopus*, a species widespread and abundant throughout the neotropics, was the most observed frugivore in pasture trees (46 visits to 13 pasture trees). I modeled the presence of 7 species, the visitation rate of 7 species and the duration of visit of 2 species.

The general pattern that emerged from models was that frugivores tended to have increased visitation to trees more distant from the forest edge and to larger crowned trees. In logistic models of frugivore presence, four species and two groups (including the group of all frugivores) were more likely to be present in trees more distant from the forest, based on the 95% credibility intervals (CI) of covariate posterior distributions

(Table 1.2). No species or groups were less likely to be present at more distant trees (based on 95% CIs). Presence was positively related to crown area for two species and Tyrannids. Neither tree cover nor AVNN index had strong correlations with presence in pasture trees (all CIs include 0), although the 95% CI for *Tyrannus melancholicus* was almost all negative for its response to percent tree cover.

Frequency of visits to pasture trees also increased in pasture trees more distant from the forest edge for three species and one family, Tyrannidae, based on 95% CIs (Table 1.3; Figure 1.2). The aggregated visits of medium-frugivory and of all frugivores increased with distance from forest edge (Figure 1.3). No species had strong negative effects for the distance parameter (all 95% CIs included zero or were positive). Visits mostly increased with increasing crown area, and one species and three groups, including total frugivores, had positive responses to crown area, based on 95% CIs. All 95% CIs of posterior distributions for AVNN index and tree cover effects on the number of visits included 0, as was the case in models of frugivore presence. However, *Tyrannus melancholicus* had a negative estimated response to percent tree cover (96% of posterior < 0), and *Tachyphonus rufus* had a positive posterior (93% of posterior > 0), although 95% CIs included 0.

The two part model indicated that distance to forest edge and crown area again had positive effects on total frugivore visitation (Table 1.4), as in the negative binomial model (Table 1.3). When analyzing the forest-frugivory index, the same two covariates had mostly positive posterior estimates. Note however, that the distance to forest covariate had a lower CI for the forest-frugivory index than for total raw visits, indicating

that the distance effect was diminished when accounting for level of frugivory and forest edge abundance (Figure 1.3d; Table 1.4). Species richness of frugivores in pasture trees increased with increasing distance from the forest edge (Figure 1.3c) and increasing tree crown area, while AVNN index and tree cover had apparently no effect (Table 1.3).

Tyrannus melancholicus spent longer time periods in pasture trees as distance from the forest increased (Table 1.5; Figure 1.4). *Thraupis episcopus* had shorter visits as distance to forest increased, although the 95% CI of the distance covariate included 0. Other covariate parameters did not show strong effects on duration of visit for these species and the aggregated visits of groups of species (Table 1.5).

I assessed whether my major results (Figures 1.2-4) were robust to the removal of the greatest observations of visitation (Figures 1.2-3), species richness (Figure 1.3c), and duration of visit (Figure 1.4). The 95% CI of the distance parameter did not include zero and remained positive even after removing the two greatest observations of visitation (Figures 1.2-3) and species richness (Figure 1.3c). However, the 95% CI for distance included zero after removing the greatest duration of visit observation of *Tyrannus melancholicus.*

DISCUSSION

Nearly all species and groups of frugivores were insensitive to the percent cover and configuration of pasture canopy cover, though I expected at least some sensitivity among species that are abundant in forest edges or uncommon in open pasture. Four species,

birds of medium frugivory, Tyrannids, total frugivores, species richness, and the forest-frugivory index all showed positive associations with the distance between pasture trees and forest edge. The forest-frugivory index, however, showed a weaker positive response to distance than did raw counts of all frugivores. No frugivore response variables had strong negative correlations to distance to forest edge (i.e. all 95% CIs included 0), which was an unexpected finding. The presence and visitation rates of species and groups of frugivores were generally higher in larger-crowned trees, which was consistent with my predictions. The patterns I observed may occur beyond the study site, as most of the study species are widely distributed in Amazonia and beyond (Ridgely & Tudor 1989, Souza 2006).

This is the first neotropical study to report a positive relationship between distance to forest edge and the visitation of multiple species of frugivores to pasture trees. Previous researchers have found both positive and negative relationships between frugivore movements and distance to forest edge, though the sign of the relationship is not clearly related to spatial scale. da Silva *et al*. (1996) found a negative relationship at distances up to 0.25 km, Luck & Daily (2003) found negative and positive relationships (depending on the species) at distances up to 8 km, Eshiamwata *et al.* (2006) found no relationship for all frugivores combined and a negative relationship for forest-dependent frugivores at distances up to 1.3 km, and Berens *et al.* (2008) found a positive relationship for distances up to 2 km. These previous studies also vary from lowland to ~1700 m elevation and were conducted in both the neo- and paleotropics, making it difficult to generalize results. Researchers have also found positive and negative

relationships between zoochoric seed rain and distance from forest, though seed rain is not perfectly correlated with visitation (Duncan & Chapman 1999, Slocum & Horvitz 2000, Cubina & Aide 2001, Ingle 2003, Zahawi & Augspurger 2006).

I did not observe declining visitation of species with distance, reduced cover, or clustering, possibly because the distribution of resources (Johnson & Sherry 2001) over-rode any spatial effects. The distribution of safe nesting sites or insects might have produced the observed correlation between visitation and distance. Frugivores might be attracted to safer nesting sites farther from the forest (Skutch 1966, Sekercioglu *et al*. 2007), though I do not have nesting data at my study site to test this possibility. Insect densities can vary with distance from forest (Landis *et al.* 2000, Rand *et al.* 2006). Many of my study frugivore species also consume insects (Fitzpatrick 1980, Ridgely & Tudor 1989) and their visitation could have been affected by spatial variation in insect density (Berens *et al.* 2008). Another possible cause of increased visitation at more distant sites is flocking behavior. Birds may be more willing to cross into open habitat when in larger groups and their groups may become more cohesive at more distant sites if risk of predation is increased (Rodriguez *et al.* 2001).

I utilized multiple quantitative measures of spatial structure of pasture tree cover to study frugivore visitation to pasture trees. The presence of two species was marginally correlated to pasture canopy cover (i.e. 95% CI included 0), while no species showed correlations to ANN index. The marginally greater importance of canopy cover in my study is consistent with studies that have found percent cover of habitat types is a better predictor of animal distributions than are measures of habitat configuration (Belisle *et al.*

2001, Bender *et al.* 2003). Species that showed the strongest marginal responses to forest cover (although 95% CIs included 0) did so in the direction expected based on reported habitat associations. The presence of *Tyrannus melancholicus*, a common species of open and canopy habitats, was negatively correlated, while the presence of *Tachyphonus rufus*, a species more typical of forest edge habitats (Ridgely & Tudor 1989, Souza 2006), was positively correlated to percent cover.

For most species, visitation to individual trees was largely unchanged even as tree cover increased, meaning that frugivores apparently used pasture trees as a resource in proportion to their availability (Johnson & Sherry 2001), although additional factors such as predation (Rappole *et al.* 1989) or dominance hierarchies (Ornat & Greenberg 2000) can limit animals' ability to track resource abundance. A previous study found that frugivore species richness increased while abundance did not vary with greater pasture tree cover levels in Nicaraguan dry forest landscapes (Harvey *et al.* 2006). Species' insensitivity to clustering of pasture trees indicates that study species were able to persist when trees were relatively isolated. Species may have foraged in short movements while at isolated trees but were apparently not averse to traveling distances on the order of 100 m when moving between trees (Robinson & Holmes 1982). I might observe distance and clustering effects on visitation if I were to expand the scale of my study. One of my study species, *Dryocopus lineatus*, is known to cross forest gaps up to 425 m (Lees & Peres 2009), and facultative frugivores of similar body size to my study species that inhabit forests and open areas in Costa Rica moved distances of several kilometers across the landscape, albeit in a matrix with greater tree cover than my site (Sekercioglu *et al*.

2007). However, most movements by my study species approach the scale of landscape I studied (da Silva *et al.* 1996). Thus the visitation patterns I observed are the outcome of daily interactions between study species and spatial structure at this scale.

My finding that large-crowned trees were more attractive to frugivores is consistent with previous studies of frugivore visitation to trees (Carlo & Aukema 2005, Zahawi & Augspurger 2006, Fink *et al.* 2009). There are a variety of mechanisms that may result in tree size being positively correlated to frugivore visitation. Animals in larger patches are less likely to encounter patch boundaries and leave patches (Bender *et al.* 2003). Larger patches present easier to hit "targets" for animals (Stracey & Pimm 2009), can offer greater protection from predators and a cooler microclimate (Manning *et al.* 2006), can harbor more diverse epiphyte communities (Flores-Palacio & Garcia-Franco 2006), and can offer greater resources to animals (Stracey & Pimm 2009). It is important to note that none of the 55 focal trees were fruiting during the study, so that fruit abundance did not vary with tree size. However, larger focal trees may have contained more insects. Species composition of pasture trees could have been an additional source of unattributed variation in visitation (Fink *et al.* 2009).

I did not find evidence that the spatial structure of pasture trees at the scale I studied (across 200 m radius plots) affects visitation of my study frugivores to pasture trees at my site. The configuration of pasture trees, whether natural or artificial (e.g. perches installed by managers seeking to attract frugivores and seed rain; Zahawi & Augspurger 2006) might have limited effects on seed rain at this scale. Nevertheless, several patterns I observed might affect zoochoric seed rain and pasture succession. First,

visitation to individual trees largely stayed constant across increasing levels of pasture tree cover. Thus pastures with greater cover likely received more visitation and possibly more seed rain per unit area of pasture because they contained a higher density of individual trees. Second, my results suggest isolated pasture trees can be important attractors of frugivores and possibly potential nuclei of succession, even up to ~200 m distant from forest edges. Third, species varied in their response to tree size and distance to forest edge. For example, the presence and visitation rates of Tyrannidae were more strongly positively related to distance from forest edge than for the Thraupidae group. This finding may be due to the greater insect preference of Tyrannidae species, and the greater fruit preference of Thraupidae species, fruit that may be of limited abundance in pastures. As a result, seeds of tree species more likely to be consumed by Tyrannidae than other groups might be deposited at greater distances in pastures.

I sampled a larger number of sites relative to some previous studies (Guevara & Laborde 1993, da Silva *et al.* 1996, Fink *et al.* 2009). However, my sampling of tree cover was limited to 20 ~6.5 ha plots, and it is likely that at larger spatial scales extreme isolation and scarcity of tree cover will lead to decreased visitation by frugivores. Further studies could use remote sensing to map the distribution of large pasture trees (e.g. Gibbons & Boak 2002) and model large-scale variation frugivore visitation to pastures (Caillaud *et al.* 2010). Tracking studies of forest-dependent frugivores that infrequently enter extensive pastures are warranted (e.g. Graham 2001), as these species may promote rare but important dispersal events.

The implications of this study are limited by the temporal extent and amount of

data I was able to collect in a three month window. Frugivory levels are higher when fruits are more abundant in the rainy season (da Silva *et al.* 1996) and it is unclear how this pattern would affect frugivore visitation in pastures. However, a previous study found no differences between seasons in spatial patterns of movement for 3 of my study species (da Silva *et al.* 1996). Tree cover and clustering might have non-linear (e.g. threshold) effects on visitation outside the range of conditions I studied. Spatial structure might influence extinction and colonization of local populations of study species over larger areas and longer time periods (Hanski & Ovaskainen 2000). Long-term studies of succession are needed to detect landscape-scale effects of variation in frugivore movements because these effects emerge over many years (Carriere *et al.* 2002b).

Researchers are increasingly recognizing the ecological role and conservation role of tree cover isolated in human-dominated landscapes (Gibbons & Boak 2002, Hughes *et al.* 2002, Manning *et al.* 2006, Harvey *et al.* 2010). Such trees provide resources for numerous animal taxa (Harvey et al. 2006) and can provide dispersal stepping stones across the matrix (Graham 2001, Gibbons & Boak 2002). I found 21 species of avian frugivores using pasture trees, many of which may depend on pasture trees (Sekercioglu *et al.* 2007). The preservation of pasture trees in the eastern Amazonian region likely will support local conservation of my 21 study species.

I studied pasture tree cover in relatively high detail. The finding of increasing frugivore visitation with pasture tree distance from forest is novel for the neotropics. This pattern extended across my study species and families of frugivores. I have demonstrated through use of fine resolution characterizations of pasture tree cover that species most

frequently crossing primary forest-pasture edges show little sensitivity to small-scale configuration and cover of pasture trees during my study.

Tables

Table 1.1. Species recorded in observations of focal pasture trees (N = 55). The total visits made during all observation periods is given, along with species abundances in the forest edge as estimated from Poisson or negative binomial models of abundance. Species with five or fewer visits to pasture trees were aggregated as uncommon frugivores in visitation models. Species with "n/a" reported for edge abundance were not recorded during forest edge point counts but were recorded in the forest edge at other times in this study. * indicates species not observed in the forest edge during this study, but that could occur there based on the literature. Frugivory level is divided into three categories: L=Low, M=Medium, and H=High.

Family	Species	Visits	Abundance in forest edge (birds ha^{-1})	Abundance model	Frugivory level	English name
Picidae	*Dryocopus lineatus*	2	0.43	Poisson	M	Lineated Woodpecker
Tyrannidae	*Camptostoma obsoletum*	10	1.7	Poisson	L	Southern Beardless-Tyrannulet
Tyrannidae	*Elaenia flavogaster*	23	2.92	neg. bin.	M	Yellow-bellied Eleania
Tyrannidae	*Empidonomus varius*	3	n/a		M	Variegated Flycatcher
Tyrannidae	*Legatus leucophaius*	1	0.85	Poisson	H	Piratic Flycatcher
Tyrannidae	*Myiarchus ferox*	1	n/a*		M	Short-crested Flycatcher
Tyrannidae	*Myiophobus fasciatus*	2	0.43	Poisson	L	Bran-colored flycatcher
Tyrannidae	*Myiozetetes similis*	15	0.72	Poisson	M	Social flycatcher
Tyrannidae	*Phaeomyias murina*	12	n/a*		M	Mouse-colored Tyrannulet
Tyrannidae	*Pitangus sulphuratus*	5	0.46	Poisson	M	Great Kiskadee
Tyrannidae	*Todirostrum cinereum*	2	n/a		L	Common Tody-flycatcher
Tyrannidae	*Tolmomyias sulphurescens*	2	0.85	Poisson	L	Yellow-olive Flycatcher
Tyrannidae	*Tyrannulus elatus*	4	1.1	Poisson	M	Yellow-crowned Tyrannulet
Tyrannidae	*Tyrannus melancholicus*	24	0.52	Poisson	M	Tropical Kingbird
Thraupidae	*Ramphocelus carbo*	9	4.32	Poisson	M	Silver-beaked Tanager
Thraupidae	*Schistochlamys melanopis*	2	n/a*		M	Black-faced Tanager
Thraupidae	*Tachyphonus rufus*	11	2.35	neg. bin.	H	White-lined Tanager
Thraupidae	*Thraupis episcopus*	46	2.66	neg. bin.	M	Blue gray Tanager
Thraupidae	*Thraupis palmarum*	19	1.89	neg. bin.	M	Palm Tanager
Fringillidae	*Euphonia minuta*	1	n/a*		H	White-vented Euphonia
Incertae sedis	*Saltator maximus*	3	2.19	neg. bin.	M	Buff-throated Saltator

Table 1.2. Posterior estimates for covariate parameters from logistic models of frugivore presence in pasture trees. 95% credibility intervals are shown; intervals in bold are those that do not include 0.

Species or group	AVNN	% Cover	Crown area	Distance
Camptostoma obsoletum	-0.9, 1.7	-1.1, 1.5	-1.2, 1.3	-0.1, 3.6
Elaenia flavogaster	-4.0, 1.4	-3.4, 1.4	**0.2, 4.3**	**0.1, 4.9**
Tyrannus melancholicus	-4.4, 2.4	-8.3, 0.1	-2.0, 2.8	**0.8, 12.0**
Tachyphonus rufus	-29.1, 20.8	-3.7, 52.9	-1.4, 7.1	**0.6, 8.6**
Ramphocelus carbo	-9.7, 13.4	-7.6, 8.3	**0.1, 8.6**	-7.0, 0.6
Thraupis episcopus	-2.6, 0.5	-1.4, 1.3	-1.1, 1.5	**0.4, 5.8**
Thraupis palmarum	-4.1, 2.7	-4.7, 2.1	**0.6, 6.8**	-2.2, 0.9
Tyrannidae	-4.1, 1.8	-4.0, 1.9	**0.2, 4.4**	**0.2, 3.9**
Thraupidae	-0.8, 0.6	-0.4, 1.0	-0.5, 0.8	-0.3, 1.1
Low frugivory	-1.1, 0.9	-0.3, 1.8	-0.4, 1.5	-0.2, 2.4
Med. frugivory	-1.4, 0.3	-0.7, 1.0	-0.1, 1.5	-0.2, 1.5
High frugivory	-1.5, 8.7	-2.3, 8.3	-0.7, 3.8	-0.4, 3.0
Uncommon spp.	-0.9, 1.1	-0.6, 1.6	-0.0, 2.0	-0.0, 2.33
All spp.	-8.3, 1.4	-2.0, 6.3	-2.8, 0.7	**1.0, 7.9**

Table 1.3. Posterior estimates for covariate parameters from negative binomial models of number of frugivore visits to pasture trees, as well as parameters from a negative binomial model of frugivore species richness in pasture trees. 95% credibility intervals are shown; intervals in bold are those that exclude zero.

Species or group	**AVNN**	**% Cover**	**Crown area**	**Distance**
Camptostoma obsoletum	-5.4, 8.9	-6.6, 9.8	-9.2, 8.7	-5.9, 10.2
Elaenia flavogaster	-3.4, 1.2	-2.5, 1.5	-0.0, 3.4	-0.6, 3.7
Tyrannus melancholicus	-0.6, 0.9	-1.9, 0.1	-0.2, 1.5	**0.6, 3.6**
Tachyphonus rufus	-2.9, 3.4	-0.5, 5.4	-2.2, 1.8	**0.0, 7.1**
Ramphocelus carbo	-3.1, 7.5	-7.5, 6.1	-2.4, 7.9	-5.8, 3.5
Thraupis episcopus	-2.3, 0.4	-2.0, 1.5	-1.0, 1.2	**0.3, 5.8**
Thraupis palmarum	-6.9, 1.6	-3.3, 4.6	**1.0, 12.0**	-4.8, 1.0
Tyrannidae	-0.5, 0.9	-0.8, 0.7	**0.0, 1.4**	**0.5, 2.1**
Thraupidae	-0.6, 0.5	-0.5, 0.9	-0.1, 1.0	-0.1, 1.1
Low frugivory	-1.4, 1.5	-0.8, 2.3	-0.8, 2.7	-0.8, 3.0
Med. frugivory	-0.5, 0.4	-0.6, 0.6	**0.1, 1.1**	**0.2, 1.3**
High frugivory	-1.2, 4.1	-1.5, 3.6	-0.6, 2.0	-0.2, 2.4
Uncommon spp.	-1.1, 1.1	-0.3, 2.0	-0.0, 2.1	-0.2, 2.3
All spp.	-0.4, 0.5	-0.3, 0.6	**0.1, 0.9**	**0.3, 1.2**
Species richness	-0.4, 0.4	-0.3, 0.5	**0.1, 0.8**	**0.2, 1.1**

Table 1.4. Posterior estimates for covariate parameters from two-part models of number of frugivore visits to pasture trees and of forest-frugivory index (visits X edge density X frugivory level). Column headings give covariate names followed by abbreviations indicating where the covariate is from the logistic or log-normal portion of the model (L = logistic, LN = log-normal). 95% credibility intervals are shown; intervals in bold are those that exclude zero.

Metric	**AVNN – L**	**AVNN – LN**	**% Cover – L**	**% Cover – LN**	**Crown area – L**	**Crown area – LN**	**Distance – L**	**Distance – LN**
Visits	-1.2, 0.4	-0.2, 0.5	-0.4, 1.4	-0.5, 0.3	-0.6, 0.9	**0.0, 0.6**	-0.0, 1.6	-0.0, 0.6
Forest-frugivory index	-1.0, 0.4	-0.3, 0.7	-0.3, 1.2	-0.5, 0.7	-0.4, 0.9	-0.2, 0.7	-0.1, 1.4	-0.2, 0.8

Table 1.5.

Posterior estimates for covariate parameters from beta-distributed models of duration of frugivore visits to pasture trees. 95% credibility intervals are shown; intervals in bold are those that exclude zero.

Species or group	AVNN	% Cover	Crown area	Distance
Tyrannus melancholicus	-1.7, 0.7	-1.8, 2.0	-2.4, 0.3	**0.9, 3.9**
Thraupis episcopus	-1.0, 1.8	-1.6, 0.6	-0.3, 2.3	-5.2, 0.4
Tyrannidae	-0.4, 0.5	-0.9, 0.4	-0.6, 0.6	-1.3, 0.4
Thraupidae	-0.4, 0.6	-0.4, 0.6	-0.2, 0.6	-0.2, 0.8
Low frugivory	-2.2, 4.7	-2.7, 2.0	-1.8, 6.4	-8.0, 3.3
Med. frugivory	-0.4, 0.3	-0.6, 0.2	-0.6, 0.3	-0.3, 0.5
High frugivory	-1.5, 2.5	-0.6, 4.0	-0.3, 1.4	-1.1, 0.5
All spp.	-0.5, 0.2	-0.4, 0.3	-0.2, 0.4	-0.2, 0.5

Figures

Figure 1.1. Simplified aerial representation of a forest edge sample site (N = 20), with pasture trees shown as dark gray circles. Frugivore visitation to three focal trees (numbered 1,2,and 3) in each site was observed. All other pasture trees of height ≥ 2 m were mapped within the semicircle of radius 200 m (light gray). The center of the semicircle was located by finding the average of the forest edge points (Xs) forming lines with the three focal trees perpendicular to the forest edge.

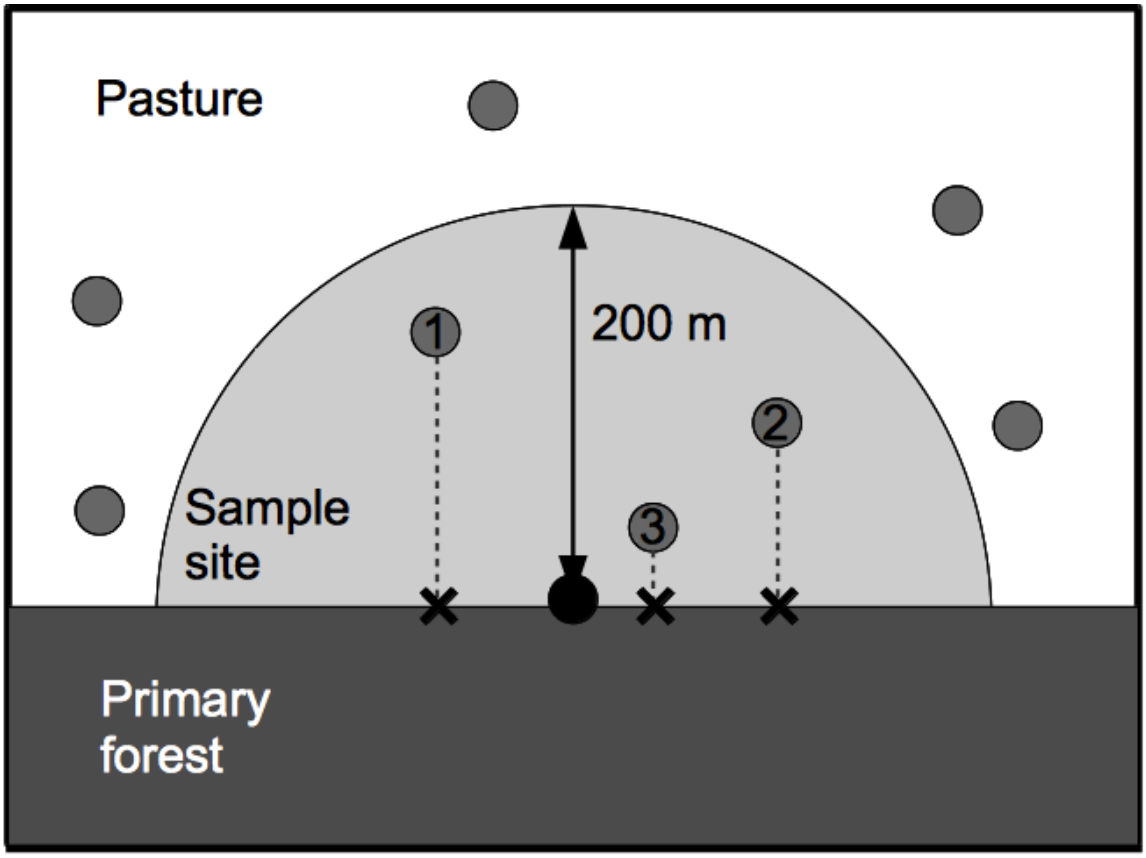


Figure 1.2. Number of visits of frugivores to focal trees vs. tree distance from forest edge for three taxa. Circles indicate observations of individual focal trees (N = 55). The curve shows the expected visits vs. distance taken from negative binomial regression, using the medians of posterior parameter distributions.

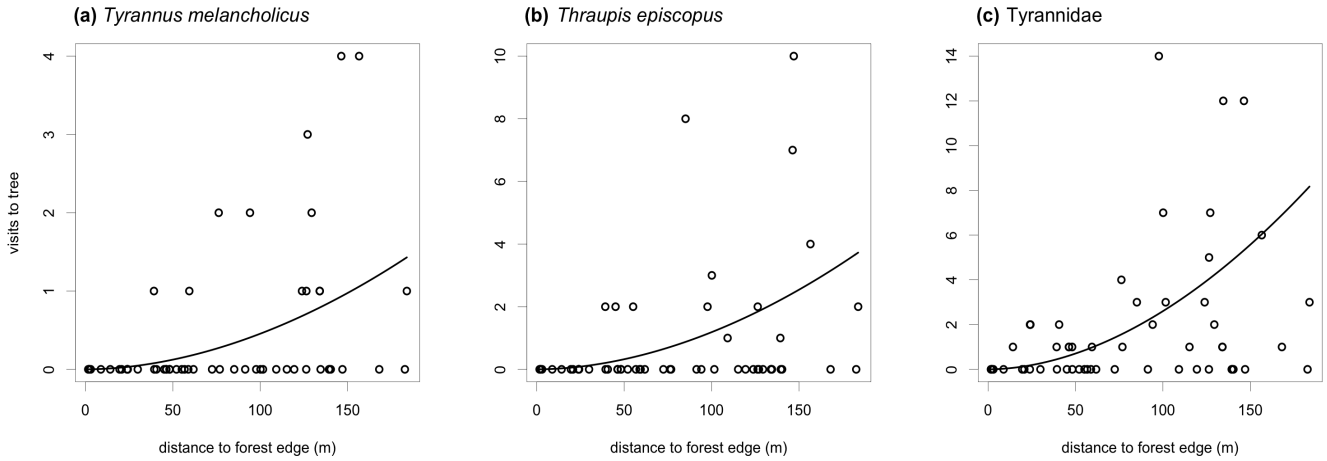


Figure 1.3. Aggregated frugivore response variables vs. tree distance from forest edge. (a) Number of visits by species of medium frugivory, (b) number of visits by frugivores of all species, (c) species richness of all frugivores at pasture trees, and (d) forest-frugivory index (visits X edge density X frugivory level) for all frugivores. The curves show the expected response vs. distance taken from negative binomial regression (a-c), using the medians of posterior parameter distributions. Circles indicate observations of individual focal trees (N = 55). In (d) the curves represent the log-normal portion of a two part model; the two dotted curves show the 95% CI values for the distance covariate, which included zero. Gray circles (d) indicate trees where no frugivores were observed and trees that are not included in the log-normal part of the model.

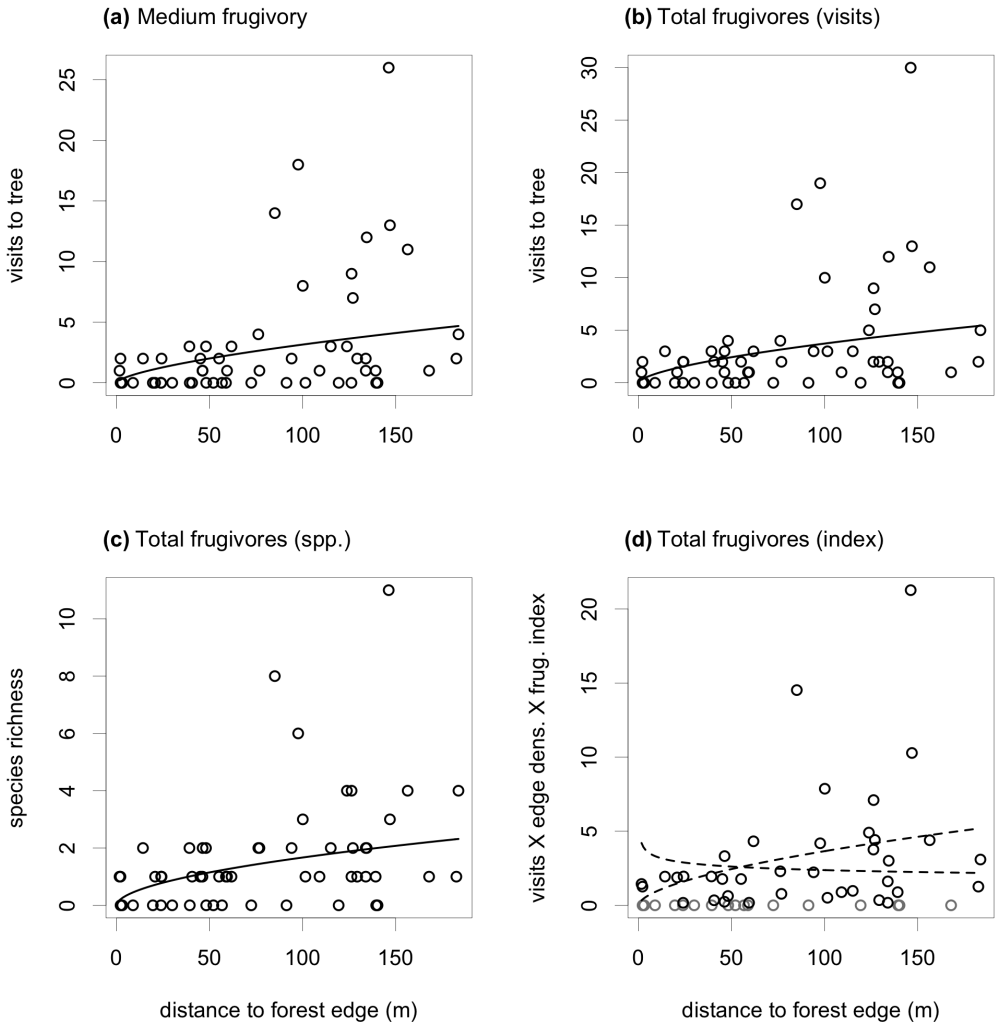
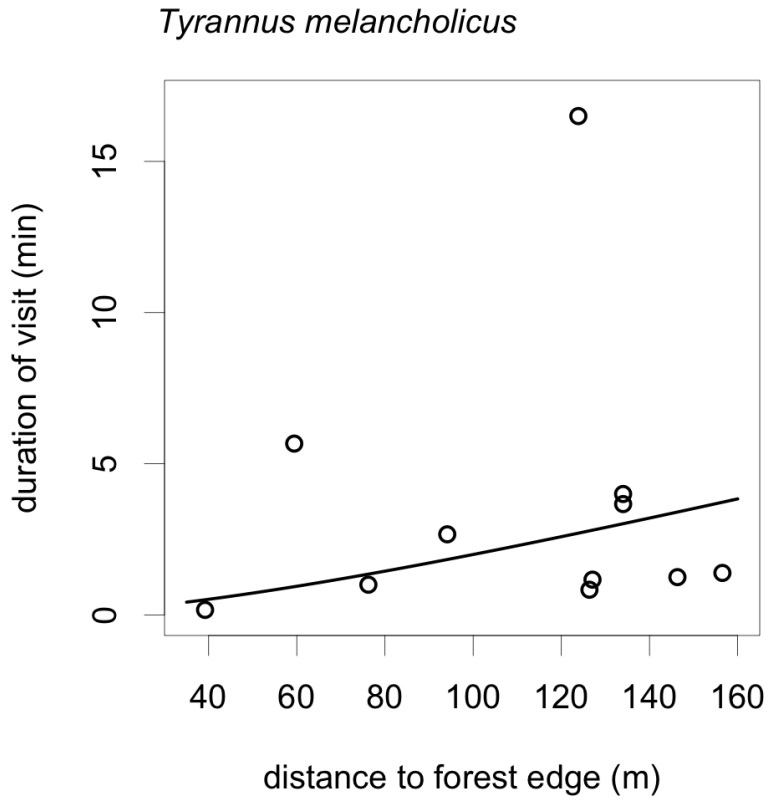

(a) Medium frugivory
visits to tree
0
5
10
15
20
25
0
50
100
150
(b) Total frugivores (visits)
visits to tree
0
5
10
15
20
25
30
0
50
100
150
(c) Total frugivores (spp.)
species richness
0
2
4
6
8
10
0
50
100
150
distance to forest edge (m)
(d) Total frugivores (index)
visits X edge dens. X frug. index
0
5
10
15
20
0
50
100
150
distance to forest edge (m)

Figure 1.4. Duration of visits by *Tyrannus melancholicus* to pasture trees vs. distance to forest edge. Circles indicate observations of individual focal trees where both the entry and exit of birds were observed (N = 11). The curve shows the expected duration of visit versus distance modeled in beta regression, using the median of the posterior parameter distribution.



Chapter II

Reserve size alters species diversity and the role of environmental limitations in simulated tree communities

INTRODUCTION

Anthropogenic habitat fragmentation can change the functional connectivity of landscapes by affecting the probability of successful dispersal from one habitat fragment to another (Gustafson and Gardner 1996). Indirect impacts of habitat loss caused by patch isolation and reduced dispersal take more time to emerge than direct impacts (Kuussaari *et al.* 2009). Variation in dispersal patterns can be a major determinant of community variation (Mouquet & Loreau 2003, Schwilk & Ackerly 2005, Gravel *et al.* 2006, Economo & Keitt 2008). Organisms dispersing from a natal patch move limited distances and the geometry of the environment determines the kind of environments they encounter (Shmida & Wilson 1985). Spatial environmental heterogeneity can affect community composition and the importance of assembly processes via effects on dispersal (Palmer 1992). However, relatively little is known from a theoretical conservation perspective about how habitat fragmentation and reserve size affect

communities structured by environmental gradients and dispersal limitation.

For an equal area of habitat loss, habitat reserves may be allocated into many small fragments at one extreme or into a single large fragment at the other extreme (*i.e.* single large or several small, SLOSS; Simberloff & Abele 1982). The effects of reserve size on community diversity were intensely debated by Diamond (1975), Simberloff & Abele (1976), and others (Higgs 1981, Margules et al. 1982, Lahti & Ranta 1985, Soule & Simberloff 1986, Burkey 1989, Ovaskainen 2002). Diamond (1975) claimed that creating a few large reserves was the best strategy to conserve the most species across reserves, which is their γ-diversity. Invoking the theory of island biogeography, he based his argument on the expectation that larger reserve "islands" have lower extinction rates, contain more species than several small reserves, and support more species with minimum area requirements (MacArthur & Wilson 1967). Simberloff & Abele (1976) and others (e.g. Higgs 1981, Soule & Simberloff 1986) countered that biogeographic theory could be invoked to support many small or few large reserves and that theory provided no clear rules for reserve design. For example, the importance of competitive exclusion in community assembly could affect whether many small reserves or a few large reserves is a better strategy (Simberloff & Martin 1991). When competitive exclusion is important, small reserve systems were expected to increase total species richness by reducing dispersal of dominant species and their exclusion of inferior competitors.

Ovaskainen (2002) used spatially explicit metapopulation theory, akin to island biogeography in its emphasis on patch area and isolation, to study reserve size effects on

occupancy and time to extinction of a single species. A few large reserves were optimal for maximal patch occupancy while more intermediate reserves maximized time to extinction. In one of the few multi-species examples using empirical demographic and dispersal data, Nicholson *et al.* (2006) studied 10 Australian species using metapopulation theory and found a set of mostly large reserves maximized time to extinction. However, it is unclear how applicable the results of Nicholson *et al.* (2006) are to other taxa as the study was not designed to test the general question of reserve size, and considered a relatively limited range of reserve sizes. The effects of reserve size on competitive ecological communities have not been well-studied. Additionally, the spatial scale of environmental heterogeneity that segregates species niches can affect community variation (Palmer 1992) and may bear on optimal reserve size strategy. Community assembly approaches that consider the limitations of dispersal and abiotic gradients could yield new insights into implications of reserve design. While previous authors have doubted whether any reserve size generalizations could emerge (Simberloff & Abele 1982), I believe that simple simulations based on a few key underlying processes may reveal how community assembly mechanisms mediate sensitivity to reserve size variation.

The unequal distribution of propagules in space affects the diversity, species abundance distributions, and drift of ecological communities (MacArthur & Wilson 1967, Wilson 1992, Hubbell 2001, Levine & Murrell 2003). Organismal dispersal limitation can generate clumped species distributions, unique local communities, and spatial turnover in community composition (Chave *et al.* 2002, Economo & Keitt 2008).

To the degree that dispersal limits local communities, unlimited dispersal among locations homogenizes communities and decreases spatial community turnover. Most communities are likely structured by both dispersal and environmental niche limitations (Tilman 2004, Schwilk & Ackerly 2005, Gravel *et al.* 2006). Dispersal is critical to species coexistence in some niche-based community models. For example, when species' niches are differentiated spatially along an environmental gradient they can coexist regionally if dispersal is sufficiently limited (Mouquet & Loreau 2003, Snyder & Chesson 2003).

Dispersal may allow non-equilibrium coexistence of species locally within an environment, even without niche differences among species. In a mass-effects or source-sink model, superior competitors coexist with sink populations of inferior competitors that persist due to propagule subsidies from source populations in other environments (Shmida & Ellner 1984, Shmida & Wilson 1985, Palmer 1992, Mouquet & Loreau 2003, Gravel *et al.* 2006). In such communities dispersal patterns are a major driver of variation in species diversity (Mouquet & Loreau 2003). Increased dispersal can increase the probability that a species will recruit and reproduce in locations where it is an inferior competitor, increasing community stochasticity and decreasing environmental limitations to communities (Gravel *et al.* 2006). When niches are differentiated across different environments, this stochasticity reduces productivity by depressing the best local competitor (Mouquet & Loreau 2003).

Sessile organisms with passive dispersal, such as trees, may commonly exhibit source-sink dynamics because of a limited ability to disperse to optimal environments

(Eriksson 1996). Source-sink local coexistence depends on the subsidy of propagules from optimal environments to suboptimal environments (Shmida & Wilson 1985). As environmental variation becomes shallower, propagules must travel farther to reach suboptimal environments, which reduces propagule subsidies that support sink populations and local coexistence (Palmer 1992). Human activity that changes the distance between environments dominated by different species may have cascading effects on such communities.

The spatial structure and dynamics of discrete patches of habitat affect dispersal patterns and community variation. A large body of research has studied how fragmentation in empirical landscapes affects community diversity (reviewed by Fahrig 2003). Empirically, the number of species harbored by a patch often increases with area (Fahrig 2003, Yu *et al.* 2012) although a number of experimental studies have failed to find such a pattern (Debinksi & Holt 2000). In simulated neutral metacommunities, edge habitats in fragmented landscapes receive fewer migrants and have low α-diversity (Chave & Norden 2007). Also in neutral metacommunities, the loss of the most highly connected patches causes the greatest change in the regional distribution of diversity because central patches are vital to maintaining regional dispersal (Economo 2011). Fragmentation research has less often addressed effects on community characteristics such as changes in the importance of different community assembly processes.

It may be instructive to study the effects of landscape structure on community assembly processes in order to predict effects in other systems based on the importance of different assembly processes. Spatial configuration of preserved habitat patches affects

potential dispersal between patches, while underlying abiotic gradients within habitat affect dispersal limitation between different environments (Palmer 1992, Gustafson & Gardner 1996). Thus degree of habitat reserve isolation can change the importance of different community assembly processes and the structure of resulting communities.

Fragmentation effects on dispersal-mediated community assembly processes likely depend on the inherent organismal dispersal ability and the scale of environmental variation. “Small” and “large” scale dispersal and environmental variation are relative terms. Changes in either the underlying scale of environmental variation or dispersal ability can have relatively similar impacts on communities (Palmer 1992, Schwilk & Ackerly 2005, Gravel *et al.* 2006). The scale of spatial autocorrelation in environmental conditions determines the difference in environmental conditions experienced by dispersing organisms relative to their natal patch (Palmer 1992). Both dispersal patterns and the level of environmental heterogeneity determine patterns in source-sink communities (Mouquet *et al.* 2006), thus I study reserve size variation in landscapes with different scales of environmental variation and across varying organismal dispersal ability.

I present the first results for how communities with source-sink dynamics along an abiotic gradient are affected by reserve size variation and associated habitat fragmentation. I propose that by affecting the dispersal of propagules across the landscape, different strategies of reserve size alter community structure. I expect that effects of reserve size will be strongest when dispersal limitation is a major factor in community assembly, *i.e.* when dispersal occurs at a small scale relative to the scale of

environmental variation. I study how increasing fragmentation in small reserve systems affects community assembly processes and a broad suite of community characteristics: spatiotemporal distribution of diversity, community determinism versus stochasticity, and productivity. To address these issues I simulated different reserve strategies on forested landscapes and analyzed reserve size effects under different scales of organismal dispersal and environmental variation.

METHODS

I used an individual-based, spatially-explicit simulation model to determine the effects of varying reserve size on highly simplified tree communities. Simulations followed weighted lottery rules of community assembly, which incorporate both dispersal and environmental limitations. In a weighted lottery, recruitment is a stochastic process dependent on the supply of propagules and environment-dependent fitness of each species (Hurtt & Pacala 1995). Individual based simulation models are useful for studying the effects of individual-scale mechanisms on the global properties of a system, even when analytical theory of the system is intractable (Grimm *et al.* 2005). I studied generic simulated tree communities undergoing fragmentation (e.g. Shugart *et al.* 1992, Hurtt & Pacala 1995, Gravel *et al.* 2006). Computer simulations of forest disturbance are also convenient because they provide faster results than physical experiments (Coates *et al.* 2003, Pearson & Dawson 2005, Uriarte *et al.* 2009).

Dispersal limitation between different environments depends on the relative scale

of organismal dispersal and environmental variation. Thus I characterized the relative scale of dispersal as the scale of dispersal divided by the scale of environmental variation. Patterns of habitat loss (which determined reserve size), environmental variation, and dispersal were all simulated as Gaussian random variables, allowing direct comparisons of the scale parameters (standard deviations σ) of the three factors.

Simulated landscapes

Landscapes consisted of a 128 X 128 cell grid (16,384 total cells) with periodic (*i.e.* wrapping) boundaries. Each cell was given an environmental value drawn from a standard Gaussian distribution. To control the spatial scale of environmental variation (*i.e.* autocorrelation) I used wavelet transformations (Keitt 2009). Wavelet coefficients *w* describe scale-specific variance in environmental structure and can be re-scaled to alter the scale of environmental variation. I conducted a 2-d discrete wavelet transform of the landscape using the 'la8' wavelet from the 'waveslim' package in R statistical software. The characteristic scale of environmental variation is determined by σ_E

$$Var(w;\sigma) \propto \exp\left(-2\sigma_E^2 f^2\right) \quad (1)$$

where *f* is the frequency or inverse scale of analysis (Keitt 2009). Wavelet coefficients were re-scaled using different values of σ_E to create landscapes with different scales of environmental variation (Figure 2.1). Larger values of σ_E generate landscapes where most environmental variation occurs across large scales and where there is little variation in environment among nearby locations. The range of values on the landscape was then re-scaled from 0 to 100 to standardize the range of conditions in landscapes.

The above wavelet transformation procedure was also used to simulate habitat loss, which controls reserve size. I generated a random surface with a specified scale of spatial autocorrelation, σ_H, as in equation 1 (Figure 2.1). Smaller values of σ_H led to low autocorrelation in habitat loss, small reserves and high fragmentation, while high values of σ_H led to highly autocorrelated habitat loss, large reserves, and low fragmentation. I thresholded values of this surface to generate a surface of habitat loss independent of the underlying environment. Cells in the top quartile of values on the habitat loss surface were kept as habitat reserves while remaining cells were deforested, resulting in habitat loss of 75%. This amount of habitat loss was sufficient to create discrete habitat fragments even when habitat loss occurred with low spatial autocorrelation.

Community simulations

Individuals competed to occupy the 'canopy' of grid cells (*i.e.* competition for space; Hurtt & Pacala 1995, Pacala *et al.* 1996). In nearly all respects, my community simulation model closely follows that of Gravel *et al.* (2006), with the added novelty that I studied community changes after habitat loss across variation in reserve size. Trees had three life stages: adults, seeds and seedlings (Figure 2.2). Only one adult could occupy a cell at a time, while local density of seedlings was not limited. I imposed a global carrying capacity on seedlings enforced by random mortality. Seedling carrying capacity was 200,000 across the landscape before habitat loss, giving an average of ~12 seedlings per cell, and 100,000 after habitat loss, giving an average of ~24 seedlings per cell. At each time step each adult randomly died with probability $P(M) = 0.25$ and created a

canopy gap in its cell (following the adult mortality rate of Gravel *et al.* 2006). When an adult died, one seedling in each grid cell was chosen based on a draw from a categorical probability distribution where species recruitment probabilities were the vector $\boldsymbol{R} = \{R_1, R_2, \ldots R_S\}$. The probability R_s of species s recruiting into a canopy gap was

$$P(R_s) = \frac{a_s}{\sum_{s=1}^{S} a_s} \qquad (2)$$

where a_s is the abundance of seedlings of species s in the cell, with S total species. Stochastic community dynamics were partly a result of this recruitment via categorical draw. Seedlings that did not recruit were allowed to remain as seedlings.

Niche-based environmental effects on community assembly were simulated at the stage of seedling survival. Twenty species occupied landscapes at the beginning of simulations, with species s differing only in their optimal environmental value μ_s (niche optimum), thus $s \equiv \mu_s$. Species niche optima were evenly spaced along the environmental axis, resulting in μ_s being separated by 5 environmental units. At each time step, seedlings perished with a probability determined by the difference between their niche optimum and the environmental value of their cell (Gravel *et al.* 2006). The probability of mortality, $P(M)$, increased with increasing difference between the niche optimum μ of species s, and the local environmental value E_i of cell i according to a Gaussian function with a standard deviation of 35

$$P(M \mid E_i, \mu_s) = 1 - \exp\left(-\frac{(E_i - \mu_s)^2}{2 * 35^2}\right) \qquad (3).$$

Seedlings in a cell with environment equal to their niche optimum, *i.e.* $E_i = \mu_s$, had $P(M)=0$. The standard deviation of equation 3 is a measure of species fundamental niche breadth and its value was chosen to allow a modest amount of stochasticity and dispersal limitation in community assembly (Gravel *et al.* 2006). At the beginning of a simulation each grid cell *i* was occupied by a single adult of the species that minimized $|E_i - \mu_s|$, defined as the best local competitor. Cells were filled with optimal species in order to begin with semi-natural distributions and to avoid dispersal limitation at the beginning of simulations (Gravel *et al.* 2006).

Dispersal patterns partly determine stochasticity in community dynamics. At each time step, adults released 5 seeds, which dispersed in random directions to distances drawn from a Gaussian density centered at zero. $P(d)$ is the probability a seed disperses distance d

$$P(d) = \frac{\exp\left(-\frac{d^2}{2\sigma_D^2}\right)}{\sigma_D\sqrt{2\pi}} \qquad (4)$$

where σ_D determines the scale of dispersal. Larger values of σ_D generated dispersal over large scales, while smaller σ_D generated small-scale dispersal. Seeds that landed in deforested matrix perished, while those landing in habitat reserves became seedlings.

Fifty generations were run with intact continuous habitat to allow dispersal patterns to affect communities in intact landscapes. After 50 generations, the habitat loss surface was imposed on the grid, and simulations were run for 350 more generations. Community metrics changed very little after 350 generations. For comparison, I

conducted additional simulations on unfragmented, intact landscapes without habitat loss.

Exploration of scale parameter space

I explored variation in three parameters, σ_H, σ_E, and σ_D, that determine reserve size, the scale of environmental variation, and the scale of dispersal, respectively. I tested an exponential series of parameter values for all three scale parameters, $\sigma = \exp(x)$, $x = \{-\infty, 0, 1, 2, 3, 4, 5, 6\}$. Five simulations were conducted for each combination of the three scale parameter values, with new habitat loss patterns and reserves generated for each simulation. I studied a reduced parameter space for effects of parameter variation on temporal community turnover, $\sigma = \exp(x)$, $x = \{-\infty, 1, 3, 5\}$.

Analyzing simulation results

I analyzed resulting landscapes and communities of adult trees with 7 measures of community assembly processes and composition (summarized in Table 2.1). I first measured spatial separation of niches, using distance as a proxy for dispersal. Here I define the niche of species *s* as all cells *i* for which μ_s gives the minimum $|E_i - \mu_s|$ among all species *S*, *i.e.* a species niche is the cells where it is the best competitor. Local coexistence in source-sink metacommunities depends on dispersal from a species' optimal environment into one where it is an inferior competitor (Shmida & Wilson 1985, Mouquet & Loreau 2003). For a given simulation with specified σ_D, seed dispersal probability from the location of an adult to any location was solely a function of distance

(equation 4), justifying the use of distance as a proxy for dispersal. Under different reserve size scenarios I calculated the spatial separation of niches, *i.e.* the distance between environments sufficiently different so as to have different optimal competitors, which is half the distance in environmental space between species niche optima (5/2 = 2.5 environmental units). For each landscape I selected random habitat cells *i* and measured the distance from *i* to the nearest cell *j* such that $|E_i - E_j| \geq 2.5$ was satisfied. I then took the average distance for 100 cells *i* in each landscape .

The second and third metrics were α and γ-species richness, respectively. α-species richness of adults was measured at the smallest scale possible, between two neighboring individual trees. The neighborhood of each cell was defined as the four adjacent cells. I randomly sampled 100 exclusive neighbor pairs from each community and calculated the average species richness of pairs ($\alpha \in [1,2]$). I calculated γ-richness as the total number of species of adults across the landscape. Note that because the range of possible alpha-richness ($\alpha \in [1,2]$) was much less than that of gamma ($\gamma \in [1,20]$), the great majority of variation in β-diversity is contained in gamma. Thus I do not present results on β-diversity, though they can be obtained by subtracting average α-richness from γ-richness (Lande 1996, Mouquet & Loreau 2003). The fourth metric was the related metric of γ-functional diversity. I calculated γ-functional diversity as the range of niche optima μ_s represented by adults on the landscape. γ-functional diversity allowed me to determine when differences in γ-richness were due to loss of species with niches at environmental extremes.

The fifth community characteristic I measured was average cell productivity, p. I considered productivity of cell i, p_i, as a function of the performance of the resident adult species given the environment, following previous authors (Tilman *et al.* 1997, Mouquet & Loreau 2003). Performance (productivity) was calculated as a Gaussian function of $E_i - \mu_s$, centered at zero, as with seedling survival (Palmer 1992). I assumed that the adult in cell i of species s was most productive if s was at its niche optimum, *i.e.* when $E_i = \mu_s$, p_i=1. Adults occupying environments far from their niche optimum were of low productivity (MacArthur & Levins 1967). Productivity of an adult in a cell was the same as the probability of survival of a seedling of that species in the cell ($p_i = 1 - P(M)$ in equation 3).

The sixth community characteristic quantified the role of environmental limitations and determinism in community assembly. Changing landscape structure and dispersal patterns might change the importance of deterministic environmental limitations. For each community I randomly sampled 100 individuals from across the landscape. I used variance partitioning (Peres-Neto *et al.* 2006) to calculate how much spatial community variation was explained by environmental gradients. I used functional community composition (*i.e.* μ_s niche optima of adults) as the response variable. μ_s are more informative than categorical species identity because μ_s are ordinal. I also explored using variance partitioning to estimate the portion of community variation explained by dispersal limitation, but available methods (Borcard & Legendre 2002) were not able to separate the contribution of environment and dispersal because of autocorrelation in the environment (i.e. nearly all community variation was explained by collinearity of

environment and spatial structure).

The last characteristic I studied concerned community stochasticity over time. When community assembly is highly stochastic, there may be greater temporal turnover in species composition even when the environment is temporally constant. I measured how μ_s of species occupying a given cell changed over time. In each community I sampled 100 cells and in each cell identified μ_s of the adults occupying the cell in the last ten time steps. I considered the variance in these ten sampled μ_s as a measure of temporal community turnover.

For each metric I tested the statistical significance of monotonic reserve size effects by comparing metrics generated for a given level of relative dispersal (σ_D/σ_E) across different reserve size scenarios. For each value of relative dispersal there were replicate simulations with different reserve sizes (i.e. scales σ_H of habitat loss). The relationship between reserve size (measured with σ_H) and the community metric of interest was tested using non-parametric Spearman's rank correlations for a given level of relative dispersal.

RESULTS

Landscape structure

When σ_H was small, many small reserves were created, habitat loss occurred at smaller scales, and remnant patches were more fragmented. Small and highly fragmented reserves had greater spatial separation of niches (i.e. environmental difference ≥ 2.5)

relative to large reserves (significant for all but one scale of environmental variation, Spearman's rank correlation, $\alpha = 0.05$ for all tests in this study; Figure 2.3). Thus when habitat is broken into small fragments, seeds have to travel farther on average to reach environments where a different species would be the best competitor, compared to distances in large reserves (Figure 2.1).

Species richness

Reserve size affected α and γ-richness. Reserve size-dependent diversity patterns were strongest when dispersal occurred at a small scale relative to the scale of environmental variation. At the three smallest non-zero relative scales of dispersal [scale of dispersal divided by environmental scale: $\log(\sigma_D/\sigma_E)$], α-richness was significantly lower in small reserves and higher in large reserves (Spearman's rank correlation; Figure 2.4A). Reserve size impacts on diversity are demonstrated in example simulation outcomes (Figure 2.5). When dispersal occurred at larger scales, the relationship between reserve size and α-richness reversed, with significantly greater α-richness occurring in small reserves (Spearman's rank correlation).

Reserve size had the effect of increasing the scale of relative dispersal at which α-richness was maximized (Figure 2.6). In intact landscapes, α had a unimodal relationship to relative dispersal, with a peak at $\log(\sigma_D/\sigma_E) = -2$. However, in landscapes with small reserves, α had a saturating relationship with relative dispersal whereby α increased with greater dispersal until about $\log(\sigma_D/\sigma_E) = 1$, beyond which α was relatively stable. In general, the effects of dispersal on α and γ-richness were strongest in small reserve

systems and diminished in large reserve systems (Figure 2.6).

γ-richness variation was monotonic and closely correlated to reserve size and the relative scale of dispersal. Small reserve systems had significantly greater γ-richness than large reserve systems under all but the three largest scales of relative dispersal (Spearman's rank correlation, Figure 2.4B). Small reserve systems harbored significantly greater γ-richness even when there was no inter-cell dispersal, *i.e.* when $\log(\sigma_D) = -\infty$. γ-richness variation was closely correlated to γ-functional diversity, as quantified with the niche range of species in the landscape (Spearman's rank correlation, $\rho = 0.99$, $p<10^{-16}$). γ-functional diversity was significantly greater in landscapes with small reserves compared to landscapes with large reserves, but only for the same dispersal scales as γ-richness (Figure 2.4C).

Community function and assembly processes

Reserve size effects on other community metrics were roughly similar to species richness, in that reserve size had its strongest effects when dispersal occurred at relatively small scales. The average productivity of a cell increased significantly as reserves became smaller, for all but four of the non-zero scales of relative dispersal (Spearman's rank correlation; Figure 2.7A).

Decreasing reserve size increased the strength of environmental limitations to community composition, as measured by the proportion of spatial community variation explained by environmental variation (Figure 2.7B). Less community variation was explained by environment when habitat was aggregated in a few, large reserves. The

increase in determinism in small reserve systems was significant for all but the three largest scales of relative dispersal (Spearman's rank correlation). Temporal community stochasticity (as measured by the variance in adult niches) in a given cell significantly increased as reserve size increased, but only at the smallest non-zero scale of relative dispersal (Spearman's rank correlation, $p<0.01$; Figure 2.8).

DISCUSSION

In this study I found that systems of highly fragmented reserves were dominated by environmental limitations to community composition and diminished effects of dispersal patterns. Reserve size variation had the strongest impact on communities when the scale of dispersal was smaller than the scale of environmental variation, which is when dispersal between environments would be a limiting factor to community composition. Fragmentation into small reserves increased spatial separation of niches and decreased dispersal between different environments, which in turn homogenized local patches and increased environmental determinism. In several respects, such as α-richness and productivity, communities in large reserve systems were most similar to intact landscapes. In other respects, such as γ-richness and γ-functional diversity, communities in small reserve systems were most similar to those in intact landscapes.

Community variation across landscapes with different reserve sizes was likely largely due to the increased spatial separation of species niches. Increasing the distance between different environments decreases the exchange of migrants for a constant level

of dispersal. The exchange of migrants between environments is essential to supporting sink populations and plays a fundamental role in determining community patterns (Palmer 1992, Mouquet & Loreau 2003, Mouquet *et al.* 2006). In mesocosm experiments, network structure that enhanced connectivity had its strongest effect on diversity when habitat was spatially heterogeneous, which is when dispersal between habitats was most limiting (Chisholm *et al.* 2011). Nearly all effects of reserve size variation weakened as dispersal became global, suggesting that limited dispersal was the mechanism of reserve size effects. With the exception of γ-diversity, all community metrics were unaffected by reserve size when there was no inter-cell dispersal (i.e. when $\log(\sigma_D)= -\infty$; Figures 2.4, 2.7, 2.8).

Dispersal rates between different environments, both due to organismal dispersal ability and reserve size, played a central role in α-richness variation. When communities are purely dispersal limited, central, highly-connected patches have highest α-diversity due to high immigration (Economo & Keitt 2008, 2010). However, communities affected by a combination of dispersal and environmental limitations exhibit more complex dynamics. My results from unfragmented landscapes were consistent with theoretical (Mouquet & Loreau 2003, Mouquet *et al.* 2006) and experimental findings (Cadotte 2006; Howeth & Leibold 2010), that dispersal and α-richness have a unimodal relationship with α peaking at intermediate dispersal. High dispersal decreases α-richness because dispersal homogenizes communities to the point where species specialized in extreme environments are driven extinct by the best average competitors across environments (Mouquet & Loreau 2003). This pattern was evident in γ-functional

diversity variation, which consistently declined in larger reserves, indicating the loss of species with extreme niches. In reserve systems after habitat loss, the correlation between dispersal and α was largely positive, whether dispersal between environments increased due the dispersal ability of trees or due to the increased proximity of different environments in large reserves (Figures 2.4A & 2.6). The lost or diminished α peak at intermediate dispersal in small reserves suggests that dispersal may have never been high enough to cause further extinctions, possibly because of the loss of propagules to the matrix. However, for some greater scales of relative dispersal, large reserves had significantly less α-richness than small reserves as expected from a unimodal dispersal-α relationship (Mouquet & Loreau 2003), though the effect was weak.

Contrary to α, γ-species richness in highly fragmented small reserves was more similar to γ in intact landscapes, likely for two reasons. First, when environmental variation is shallow and autocorrelated across large scales, a widely dispersed set of reserves was required to capture the range of environments present in the landscape. The increase in γ-richness with wider environmental sampling was demonstrated by the increase in γ in small reserves even when there was no inter-cell dispersal (when $\log(\sigma_D)= -\infty$ in Figure 2.4B). Spatial autocorrelation of environmental conditions is pervasive in natural landscapes. However, the spatial sampling effect of small reserves on γ depends on the segregation of species niches along those environmental gradients. Thus the spatial sampling effect depends on spatial autocorrelation in environmental niche axes. Authors have previously argued that many small reserves should have greater spatial sampling of species (Simberloff & Abele 1976), and that spatially random habitat

preservation better samples γ-richness (Seabloom *et al.* 2002). Likewise, the use of complementarity indices to maximize γ-richness in reserves often prioritizes a large number of fragmented reserves (Margules & Pressey 2000, Economo 2011).

Dispersal limitation also contributed to increased γ small reserve systems. Increasing σ_D from zero to small-scales magnified the increase in γ-richness in small reserves (Figure 2.4B). Thus the high γ-richness in small reserve systems is due to both dispersal limitation and spatial sampling. Species that specialized in extreme, uncommon environments were the source of extinctions in large reserves, indicating that as spatial niche separation decreased and dispersal increased the best average regional competitors excluded other species. The effect of dispersal on γ as the best average competitors dominates has been demonstrated in previous work (Palmer 1992, Mouquet & Loreau 2003, Cadotte 2006) and was as a previous argument against a large reserve strategy (Simberloff & Abele 1976, Soule & Simberloff 1986).

In landscapes with greater disturbance and smaller population sizes, extinction-colonization dynamics of patches may become more important. In my simulations nearly all habitat cells were occupied and communities with low dispersal ability in small reserves were dominated by the best local competitors. On the other hand, when disturbance rates are higher and there are many unoccupied patches, small reserves will likely have lower colonization rates, such that the best local competitor may rarely be present and environment will play reduced role in community variation (Horn & MacArthur 1972). While smaller reserves in my study maintained more species across simulated landscapes, real forested landscapes may suffer from more frequent

disturbance at fragment edges that could change my results (Laurance *et al.* 1998). High temporal frequency disturbances can eliminate the gains in γ-diversity in fragmented landscapes (Roy *et al.* 2004). When species are able to evolve in response to local conditions, low dispersal between small reserves could reinforce the dominance of the best local competitors (Loeuille & Leibold 2008). In landscapes without spatial environmental variation, spatially contagious (as opposed to random) disturbances decrease the risk of stochastic extinction (Ovaskainen 2002), though I expect an opposite effect of contagious disturbance in my system because of high autocorrelation in environment and species distributions. Bimodal relationships between dispersal and γ-diversity can occur under temporal environmental variation in fragmented communities (Loreau *et al.* 2003).

At all but the largest dispersal scales, communities in small reserves were more environmentally deterministic and tended to be dominated by the best local competitor. Increased dispersal between environments in large reserves homogenized communities and thus the environment played a reduced role in structuring communities (Mouquet & Loreau 2003, Schwilk & Ackerly 2005, Gravel *et al.* 2006, Mouquet *et al.* 2006). Temporal community turnover was lower in small reserves, albeit for a limited set of conditions. In a metacommunity of larval amphibians, ponds with greater connectivity to other ponds showed greater temporal community turnover, supporting the role of landscape structure controlling dispersal and thus community stochasticity (Werner *et al.* 2007). To the contrary, a long term grassland experiment showed greatest temporal turnover in small patches, which the authors attributed to greater stochastic extinction

due to low population sizes in small patches (Cook *et al.* 2005). However, dispersal distances in this system may have been sufficiently large to overcome dispersal limitation among patches, which should reduce the effects of patch area. The changing importance of environmental limitations versus stochastic dispersal limitation is rarely quantified in assessments of anthropogenic impacts. However, stochastic dispersal that maintains α-diversity in one functional group, such as trees, may be important to the conservation of diversity in an interacting group, such as frugivores (Kissling *et al.* 2007).

The increased dominance of the best local competitor in small reserves was responsible for increased productivity in smaller reserves. In community models where species niches are differentiated spatially across environments (as opposed to locally within environments), increasing local diversity tends to decrease productivity because additional species are sink populations of inferior competitors (Mouquet & Loreau 2003). This negative diversity-productivity relationship is known as a negative selection effect (Loreau 2010). My results show that the negative selection effect decreased in smaller reserves. When species niches are differentiated locally within an environment, more diverse communities tend to be more productive partly because species limit themselves more than each other, causing over-yielding (MacArthur & Levins 1967). Additionally, temporal environmental variation can cause positive diversity-productivity relationships in heterogeneous landscapes when dispersal provides spatial community "insurance" across different temporal environmental fluctuation (Loreau *et al.* 2003, Gonzalez *et al.* 2009). The degree to which spatiotemporal niche differentiation across environments versus local niche differentiation explain species coexistence will partly

determine the strength of reserve size effects on productivity. The cascading effects of landscape change on community processes and properties such as productivity merit further investigation because of this possible dependence on axes of niche partitioning. Dispersal between different environments is also an important determinant of local adaptation and the evolution of specialization (Behrman & Kirkpatrick 2011, Urban 2011), and future work should examine how reserve size variation affects patterns of local adaptation.

Source-sink communities, where local coexistence is supported by dispersal, may be more sensitive to fragmentation into small reserves that reduces dispersal compared to communities where local coexistence is due to niche-partitioning within an environment. Factors that reduce source-sink dynamics, such as directed dispersal to optimal environments, may reduce the reserve size effects I observed. However, the importance of source-sink dynamics and their role in driving natural diversity patterns is poorly known. The fact that the importance of dispersal is poorly known for most communities represents a huge challenge for land-use planning in conservation because dispersal is strongly affected by landscape change (Economo 2011)

I acknowledge that model simplification may prevent my simulation from capturing some aspects of real forests, such as increased disturbance at their edges. The demographic parameters used in my model are not representative of any specific community, thus the strength of reserve size effects will likely change among systems. The amount of habitat lost can affect which reserve size strategies are optimal for metapopulations (Ovaskainen 2002). Nevertheless, my model provides novel results

about potential impacts on community structure and assembly under different reserve size strategies.

Conclusions

My results shed light on previously under-studied aspects of reserve size variation, but are not intended to determine a single, universally applicable reserve size strategy (Ovaskainen 2002). Overall, my results indicate trade-offs in fragmented community patterns along a reserve size axis, with α-richness and community stochasticity enhanced in large reserves and γ-richness, productivity, and environmental limitation enhanced in small reserves. I demonstrated that reserve size, fragmentation, and the scale of habitat loss can impact many characteristics of communities and their assembly mechanisms. These potential impacts should be considered in conservation evaluations. For example, if a pollinator community depends on year-round floral resources from a diverse forest community, breaking a landscape into small forest reserves may change the distribution of plant diversity, and hence the spatiotemporal distribution of floral resources. Communities where diversity is most strongly influenced by dispersal may be most sensitive to reserve size variation.

Tables

Table 2.1. Measures of community composition and assembly processes.

Community characteristic	How calculated
1. Spatial separation of niches	Average distance from a habitat cell to the nearest cell where the environmental difference between cells ≥ 2.5
2. α-species richness	Average species richness of two neighboring trees
3. γ-species richness	Total species found on the landscape
4. γ-functional diversity	Range of environmental niches of species found on the landscape
5. Productivity	Gaussian function of the how well matched the average adult is to its cell environment (productivity = $1 - P(M)$ from equation 2)
6. Proportion of community variation explained by environment	Proportion of spatial variation in adult composition explained by cell environmental values, using variance partitioning (Peres-Neto et al. 2006)

Figures

Figure 2.1. Examples of the range of random, wavelet-generated landscapes studied. Landscapes ranged from those with small-scale environmental variation (top row) to large-scale variation with high spatial auto-correlation (bottom row). As the scale of habitat loss increases from small (middle column) to large (right column), reserve size increases and fragmentation decreases (small reserves in middle column, large reserves in right column).

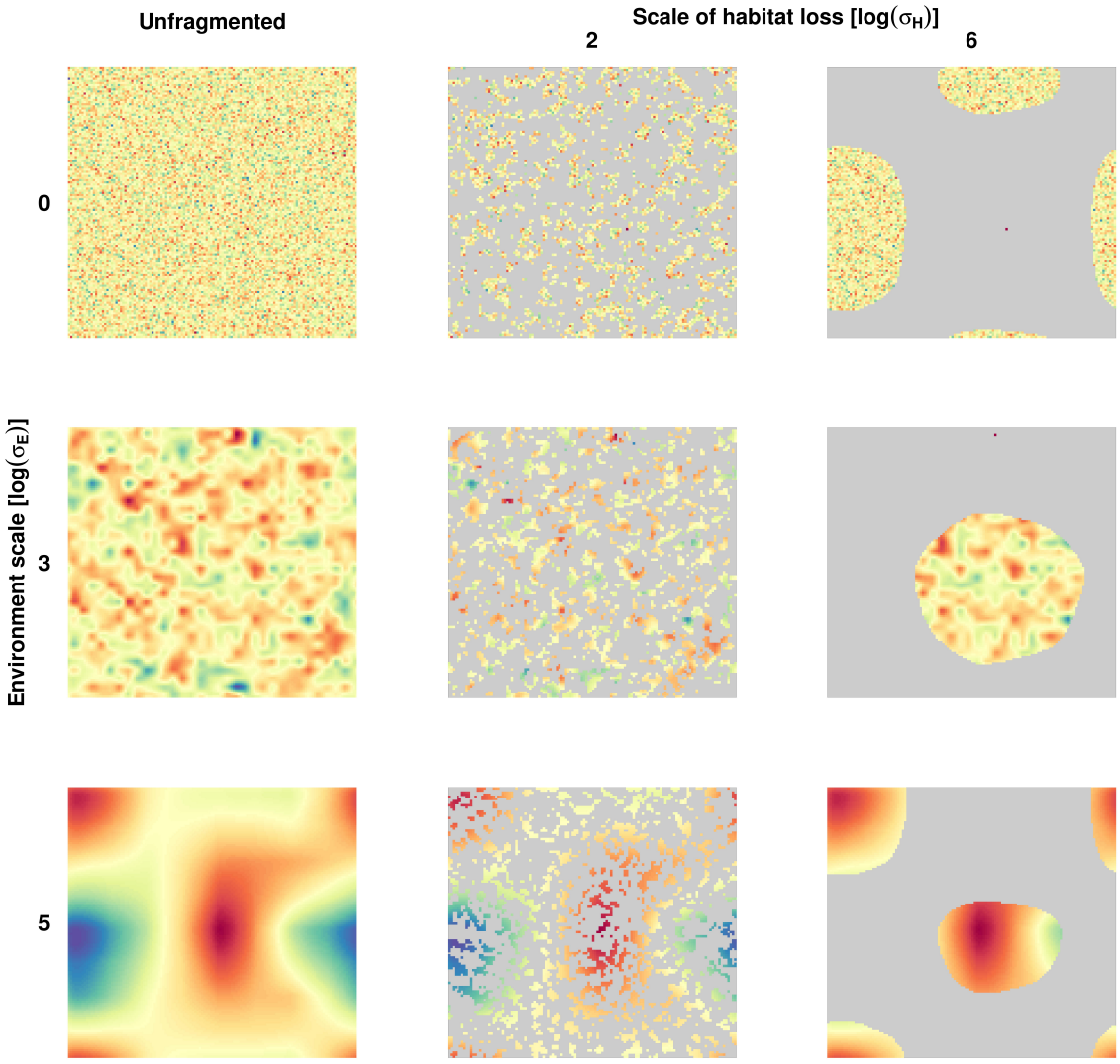


Figure 2.2. Life cycle of simulated trees. Processes described by gray arrows were neutral with the respect to species identity. The black arrow indicates seedling survival, which was the only process that varied depending on species identity and the local environment.

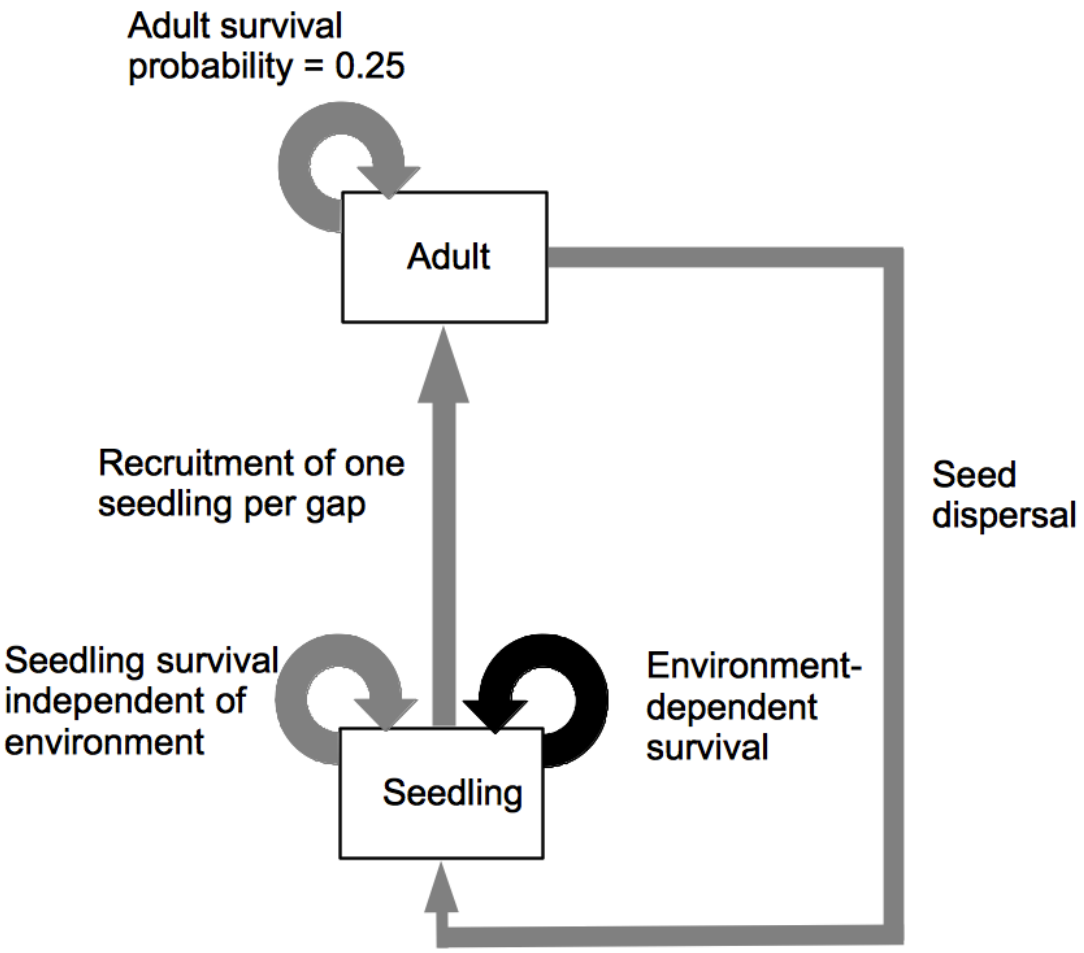


Figure 2.3. Spatial niche separation (the distance from a given cell to the nearest cell of a different environment) increased in smaller reserves, *i.e.* at smaller scales of habitat loss. A different environment is defined as one that has an environmental value distinct enough so that a different species is the best competitor (environmental difference between cells ≥ 2.5). Asterisks indicate the significance of the reserve size effect, which is the correlation between distance to different environment and the scale of habitat loss (Spearman's rank correlation, '.' p < 0.1, '*' p < 0.05, '**' p < 0.01, '***' p < 0.001).

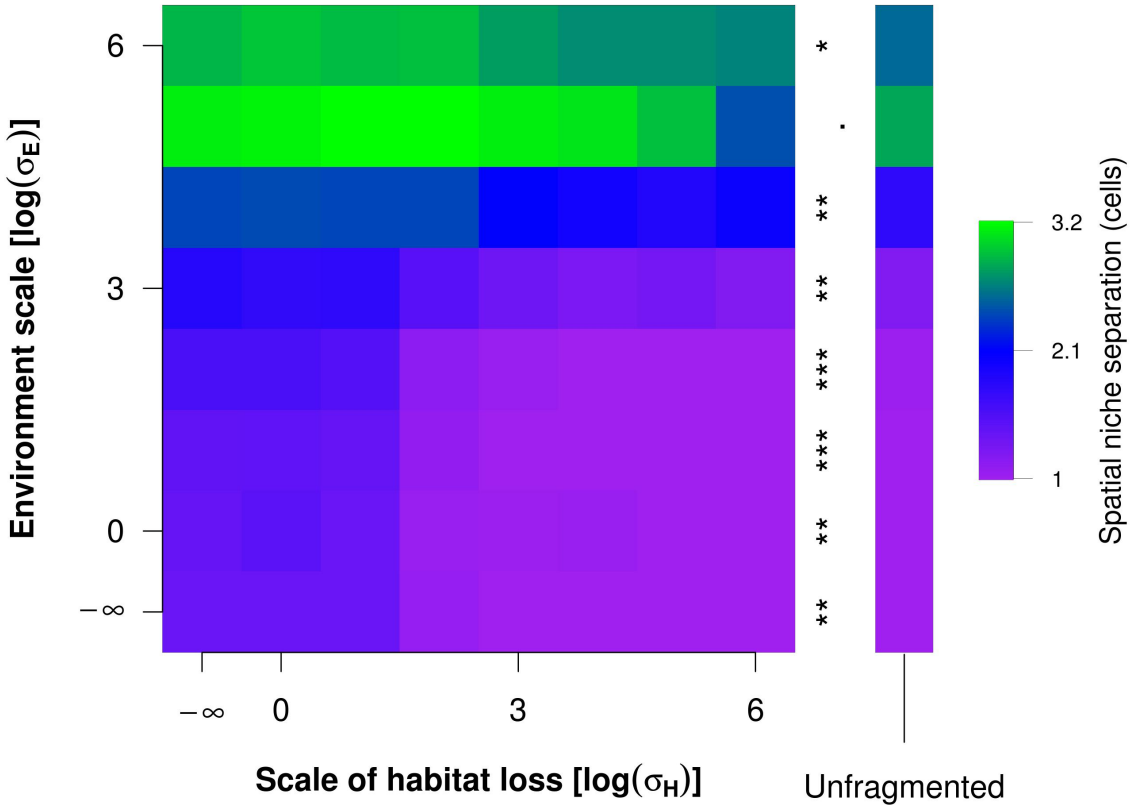


Figure 2.4. The change in diversity patterns across landscapes of varying reserve size (scales of habitat loss, x-axes) and relative scales of dispersal (relative to environment, y-axes). A and B show α and γ-species richness, respectively. α-richness is measured as the average richness of two neighboring adults. C shows the γ-functional diversity, *i.e.* the range of environmental niches represented by species on the landscape. Asterisks indicate the significance of the reserve size effect, which is the correlation between the diversity response variable and the scale of habitat loss (Spearman's rank correlation, '.' p < 0.1, '*' p < 0.05, '**' p < 0.01, '***' p < 0.001).

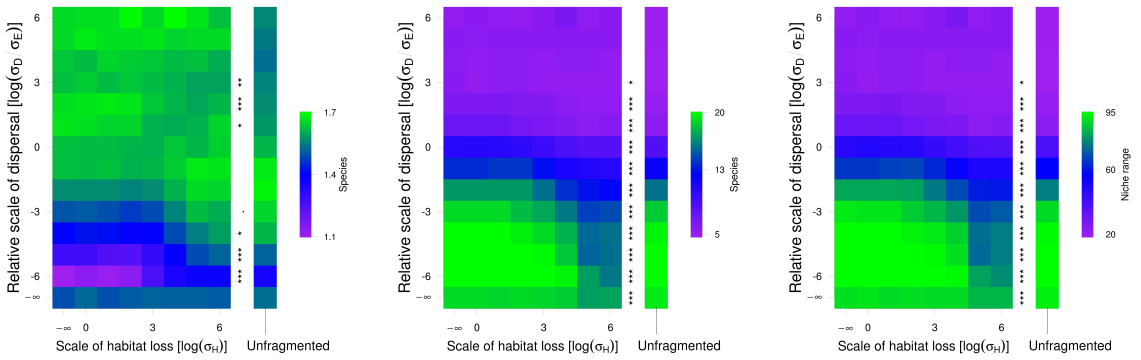


Figure 2.5. Comparisons of three different habitat loss scenarios for the same landscape, showing how reserve size affects diversity patterns. In these simulations the scale of dispersal (σ_D) = 1. Deforested areas are shown in gray. Individual trees are represented as dots of different colors, with color indicating different species with different environmental niches. Note that similar colors here do not indicate similar niches of different species. This was done in order to improve visualization. Note that smaller reserves (left) tended to be dominated by the best local competitor.

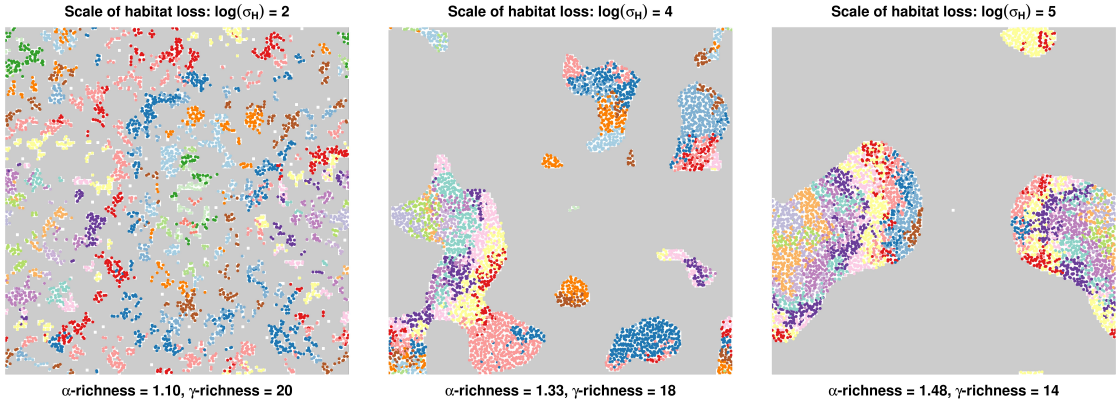


Figure 2.6. The change in the effects of dispersal on communities under different reserve sizes. In unfragmented landscapes, there was a unimodal relationship between α-richness and relative dispersal. In small reserve systems (e.g. $\log(\sigma_H) = -\infty$), there was a strong monotonic increase in α with greater dispersal. Both α and γ-richness showed weaker responses to increased dispersal when in large reserves (e.g. $\log(\sigma_H)=6$). Vertical bars show standard errors.

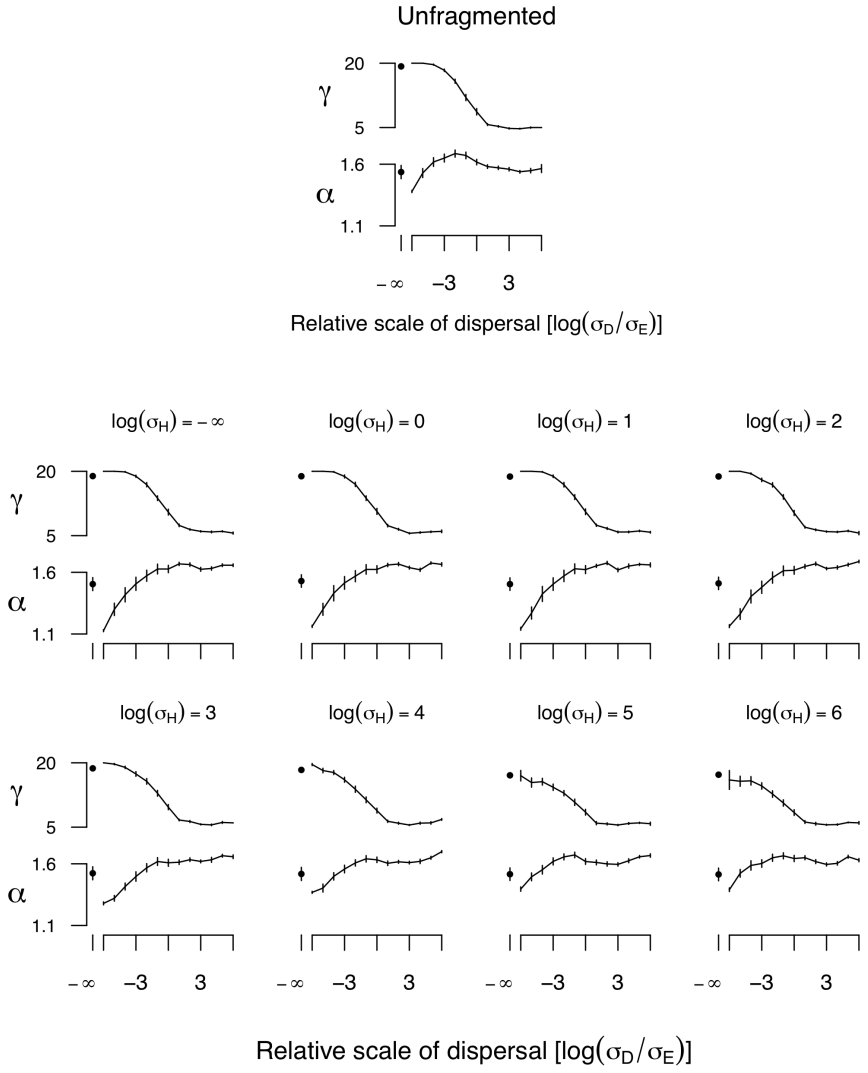


Figure 2.7. The change in productivity and environmental determinism across landscapes of varying reserve size (scales of habitat loss, x-axes) and relative scales of dispersal (y-axes). A – Proportional productivity is measured as a fraction of the maximum possible, which is attained by the best competitor for a given environment. B - The proportion of community variation explained by environmental variation using variance partitioning. Asterisks indicate the significance of the reserve size effect, which is the correlation between the diversity response variable and the scale of habitat loss (Spearman's rank correlation, '.' p < 0.1, '*' p < 0.05, '**' p < 0.01, '***' p < 0.001).

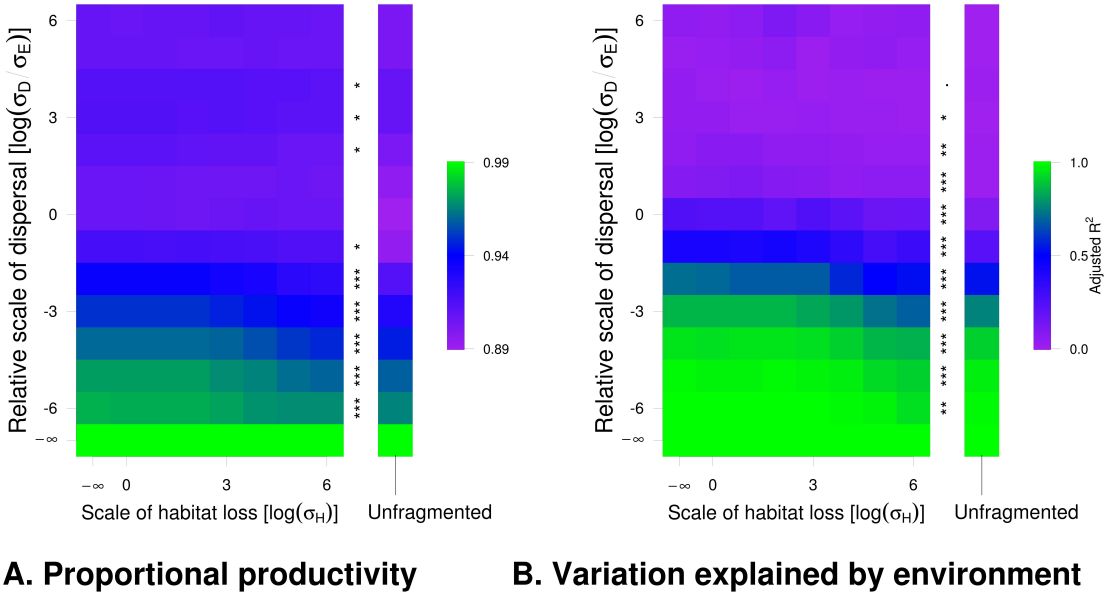
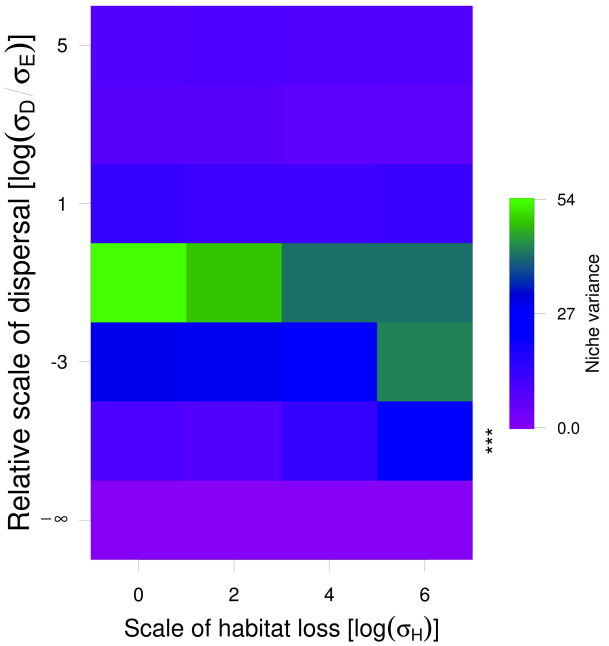


Figure 2.8. The change in temporal community stochasticity across landscapes of varying reserve size (scales of habitat loss, x-axes) and relative scales of dispersal (y-axes). Temporal turnover is measured at the level of individuals occupying the same cell, across 10 generations at the end of simulations. Asterisk indicate the significance of the reserve size effect, which is the correlation between the diversity response variable and the scale of habitat loss (Spearman's rank correlation, '***' $p < 0.001$).



Chapter III

The role of functional traits and individual variation in the composition of *Ficus* assemblages

INTRODUCTION

The identification of processes promoting spatial community variation and species coexistence is a central goal in ecology. Variation in abiotic and biotic environments can impose selective gradients on ecological communities, which can generate spatial variation in communities and over longer time scales can generate evolutionary changes in the species of a community. A developing approach to the study of community variation is the use of functional traits to estimate variation in how organisms interact with their environment, which is an aspect of niche variation. Functional traits link life history to environment and reflect axes of niche variation (McGill *et al.* 2006). Trait diversity patterns may bear the signature of different processes underlying spatial variation in communities (Tilman 1982, 2004, Weiher & Keddy 1995). Trait diversity patterns can be used to identify the specific trait and abiotic axes associated with niche-

based community variation (Cavender-Bares *et al.* 2006, Cornwell & Ackerly 2009). The large majority of trait-based studies of coexistence assume in analyses that individuals of a species have identical traits and niches. However, intraspecific variation is often extensive, with wide-ranging ecological implications (Bolnick *et al.* 2011, Violle *et al.* 2011). I studied individual-level trait diversity in assemblages of an ecologically important and diverse genus, *Ficus* (Moraceae), in order to infer variation in the processes underlying spatial variation in assemblages.

Intraspecific functional trait variation

Intraspecific functional trait and niche variation can play an important role in determining community structure and species coexistence. Intraspecific variation affects the outcome of interactions with heterospecific neighbors (MacArthur & Levins 1967, Lichstein *et al.* 2007, Bolnick *et al.* 2011, Pruitt & Ferrari 2011, Schreiber *et al.* 2011, Violle *et al.* 2011, Genung *et al.* 2012) and can also be a consequence of interspecific interactions (Mraja *et al.* 2011). High intraspecific variability increases species niche widths, which can allow species with more similar niche means to coexist (MacArthur & Levins 1967) and reduce competition among neighbors because of less niche overlap among individuals (Vellend 2006, Bolnick *et al.* 2011). Recently, there has been progress in inferring community assembly processes based on trait diversity measured at the individual level (Jung *et al.* 2010, Paine *et al.* 2011). However, this still-emerging field could benefit from additional research.

From a technical perspective, ignoring intraspecific variation can result in

inaccurate estimation of trait and niche differences of co-occurring organisms (Jung *et al.* 2010), which may reduce power to reveal community assembly mechanisms (Paine *et al.* 2011). Intraspecific patterns might differ in the sign of trait signal among co-occurring species, for example when there is low trait diversity among co-occurring species but low high diversity among co-occurring individuals. Additionally, species may differ in the magnitude of intraspecific variability, so that extrapolating intraspecific patterns across species may give inaccurate estimates of niche variation (Albert *et al.* 2011).

Ficus *as a model of species coexistence*

The diversity of *Ficus* (figs, Moraceae) assemblages is representative of the diversity of lowland tropical rainforests in general (Harrison 2005). *Ficus* is the only genus diverse in lowland tropical forest sites worldwide, with approximately 800 species (Berg 1989, Harrison 2005). Additionally, *Ficus* was the most diverse genus in nearly all complete Paleotropical lowland rainforest florulas (including at my study site in southwest China), being most speciose in southeast Asia-Pacific (Berg 1989, Harrison 2005). Like many tropical rainforest tree species, *Ficus* species are often very rare (Berg 1989, Harrison 2005). *Ficus* species are a keystone group to maintaining tropical rainforest diversity because of their year-round fruiting and role in supporting frugivore communities (Terborgh 1986, Lambert & Marshall 1991, Shanahan *et al.* 2001, Kissling *et al.* 2007). For these reasons *Ficus* is a model group for understanding tropical forest biodiversity and species coexistence (Harrison 2005).

Most *Ficus* research has focused on reproductive ecology and close symbioses

with pollinators, parasites, and seed dispersers (for reviews see Shanahan *et al.* 2001, Machado *et al.* 2005, Herre *et al.* 2008). Similarly, hypotheses for the high global species richness and α-diversity of *Ficus* have focused on high speciation rates due to specialized pollinators and low interspecific competition due to low competition for pollinators (Janzen 1979, Herre *et al.* 2008). Fewer studies have investigated additional mechanisms that may promote coexistence, such as resource use and local niche partitioning (but see Harrison *et al.* 2003, Harrison & Shanahan 2005, Hao *et al.* 2011).

Inferring community assembly from trait diversity

Trait diversity of co-occurring organisms is considered to provide evidence for one of two types of opposing niche assembly axes (Amarasekare 2003). First, biotic interactions may create local niche differentiation via competitive exclusion of competitors with similar niches (MacArthur & Levins 1967, Tilman 1982, Pacala & Tilman 1994, Tilman 2004) or when other density-dependent processes such as parasitism act on organisms with similar niches (Kembel & Hubbell 2006). Local niche differentiation within an environment is expected to generate trait over-dispersion among co-occurring organisms. Second, spatial niche differentiation across environmental gradients, where the environment imposes selection or filtering on organisms based on their traits, is expected to cause low diversity and clustered traits of co-occurring organisms (Weiher & Keddy 1995). Pure dispersal limitation in a neutral model can generate variation in trait diversity even if traits have no ecological effect (Swenson & Enquist 2009). A neutral model of assembly assumes that species are ecologically and demographically equivalent (Hubbell

2001), and as such, species distributions should be unaffected by species traits.

Trait patterns of co-occurring species can provide information on the scale of species interactions with the abiotic and biotic environment and the specific trait axes associated with niche variation (Cavender-Bares *et al.* 2006, Swenson & Enquist 2009, Kraft & Ackerly 2010, Pinto & MacDougall 2010, Violle *et al.* 2011). The role of niche differentiation in structuring communities may change across spatial scales, either because competitive interactions are restricted in space (in the case of local niche differentiation), or when the environment varies at scales smaller than the grain of analysis (Webb *et al.* 2002, Cavender-Bares *et al.* 2006, Swenson *et al.* 2007, Swenson & Enquist 2009).

Empirical trait-based studies support the importance of both types of niche assembly. For example, more than one pattern of trait diversity may occur on different trait axes at the same time (Weiher *et al.* 1998, Tofts & Silvertown 2000, Cornwell & Ackerly 2009, Uriarte *et al.* 2010), resulting in a wide spectrum of trait diversity patterns within a forest plot (Kraft *et al.* 2008, Swenson & Enquist 2009). Environmental conditions may determine the importance of spatial niche differentiation though few studies have explored this hypothesis (but see Cornwell & Ackerly 2009), especially for tropical forests. When abiotic factors are harsh and limiting to population growth, biotic processes may become less important (Chase 2007). In harsh environments, abiotic filters may generate low trait diversity of co-occurring organisms and greater spatial niche differentiation (Cavender-Bares *et al.* 2006). For example, soil moisture shows strong variation along topographical gradients (Daws *et al.* 2002), which correspond to

major niche axes in tropical forests (Engelbrecht *et al.* 2005).

I studied how functional trait diversity explained *Ficus* distributions across a 20-ha forest plot. I expected that individual level trait diversity among co-occurring trees would exhibit stronger, and possibly different, effects of niche assembly compared to species-level analyses. I expected that harsh environments would be associated with low trait diversity and evidence for stronger spatial niche differentiation. Finally, I expected that trait patterns caused by niche assembly would weaken with spatial scale.

METHODS

Study site

My study site was the 20-ha tropical seasonal rainforest dynamics plot in Xishuangbanna prefecture, Yunnan Province, China (21°36'50" N, 101°34'36" E) at 765 m asl (range: 709-869 m asl). Fourteen km from the plot, Mengla County receives 1,531.9 mm yr^{-1} rainfall (Zhu *et al.* 2006, Lan *et al.* 2009). Approximately 85% of rain falls during a 6 month period (Cao *et al.* 2006). Mean annual temperature is 21^{o}C (Zhu *et al.* 2006). Soils in the elevational band of the forest plot are laterite, derive from siliceous rocks, and have deep solum but thin humus (Cao *et al.* 2006). The plot is dominated by the emergent *Parashorea chinensis* (Dipterocarpaceae) that reaches 60 m tall and occurs near the northern limit of Dipterocarp rainforests (Zhang & Cao 1995, Lan *et al.* 2009). The plot measures 400 x 500 m (Cao *et al.* 2008).

Three topographical variables were studied and were measured by personnel at

Xishuangbanna Tropical Botanical Garden (XTBG). Elevation was measured at the corners of 10 m quadrats. Convexity was calculated as the elevation of a quadrat minus the mean elevation of the eight neighboring quadrats. I calculated slope as the mean angular deviation from horizontal of each of the four triangular planes formed by three quadrat corners.

In 2007 all arborescent stems ≥ 1 cm diameter at breast height (1.3 m; DBH) were mapped, measured for DBH, and identified by XTBG staff following established protocol (Condit 1998). The census recorded 111,177 stems belonging to 469 species and morphospecies of uncertain taxonomy. *Ficus* was the most species rich genus on the plot having 19 identified species and 3 morphospecies. There were 3,221 *Ficus* stems, which comprised 2.9% of stems and 4.6% of the total basal area on the plot (Table 3.1). *Ficus* species are also some of the most abundant in the soil seedbank in this forest (Tang *et al.* 2006). *Ficus* stems were densest along the steep slopes of the plot, and less dense along ridges and at the bottom of ravines (Figure 3.1).

Trait sampling

I sampled four leaf traits and two additional traits that may correspond to niche and life history variation: 1) leaf succulence [(fresh weight – dry weight)/area], 2) specific leaf area (SLA, leaf area / dry weight), 3) leaf area, 4) syconium (*i.e.* the pseudocarp containing multiple *Ficus* fruits) diameter, and 5) maximum DBH, and 6) leaf latex exudation (fresh latex weight exuded / width of leaf cut; Tables 3.2 & 3.3). Three traits: leaf succulence, leaf area, and SLA, were sampled for many individuals on the plot and

were analyzed at the individual-level. These traits correspond to a variety of niche axes.

Leaf succulence corresponds to a trade-off between leaf life span versus leaf productivity (Garnier & Laurent 1994). SLA variation corresponds to a trade-off between photosynthetic rate and cost of leaf growth (Wright *et al.* 2004). Leaf area variation trades off between increased light capture by large leaves and increased cooling in small leaves (Dolph & Dilcher 1980). Size variation in *Ficus* syconia corresponds to variation in associated frugivore assemblages (Githiru *et al.* 2002, Lómascolo *et al.* 2010). Syconia size also corresponds to an axis of differential reproductive investment strategies and mutualist pollinator rewards (Herre 1989). Maximum DBH is a proxy for maximum height (Kraft & Ackerly 2010), which represents variation in the light niche of adults (King *et al.* 2006).

Latex exudation by damaged leaves plays an important role in herbivory defense, and quantification of exudate may be a direct measure of herbivory defense strategy (Rasmann *et al.* 2009). Latex often contains high concentrations of secondary metabolic compounds involved in defense and can impede herbivores by sticking to their bodies or sticking up mouthparts (Agrawal & Konno 2009). Latex exuding plants and their herbivores have become a model system for understanding the ecology and evolution of plant-herbivore interactions (Agrawal & Konno 2009). Traits directly involved in biotic interactions, such as latex exudation, may show strong effects of local niche differentiation if neighbors with similar traits share herbivores that mediate indirect competition (Chaneton & Bonsall 2000). *Ficus* presents an attractive system for this topic because nearly all *Ficus* (and Moraceae) species produce latex, a trait that is often

associated with highly diverse lineages (Farrell *et al.* 1991). *Ficus* phytophagous insect assemblages overlap among *Ficus* species, thus co-occuring individuals may interact indirectly via herbivore interactions (Basset & Novotny 1999).

Leaf data were collected from individuals on the 20-ha forest plot and growing at XTBG. I collected leaf traits for both species and individual-level analyses. I attempted to sample at least 5 individuals of each species, however, because some species were rare on the plot, too large to collect with pole shears, and were absent from XTBG, I was unable to collect 5 for every species (Table 3.1). I collected three mature, sun-exposed leaves from each individual, and processed leaves in the afternoon on the same day they were collected (Cornelissen *et al.* 2003). I also targeted all individuals with DBH ≥ 10 cm on the plot. XTBG staff used 13 m pole shears and were able to reach 15 m into the canopy to collect leaves for these larger individuals. However, I was limited to sampling 335 of 521 (64%) individuals with DBH ≥ 10 cm because of the limited length of the shears.

Syconium diameter of identified species was obtained from published species accounts (Wu *et al.* 2003). I followed previous approaches to reducing sampling bias in maximum DBH estimates (King *et al.* 2006, Kraft *et al.* 2008). For maximum DBH of each species I took the average of the top 3 individual DBHs for species with over 500 individuals, the average of the top 2 DBHs for species with 100-500 individuals, and the top DBH of species with less than 100 individuals. All traits were highly right-skewed and I log-transformed them for analyses, except for SLA.

I used a recently developed assay with slight modifications to measure

interspecific variation in latex exudation (Rasmann *et al.* 2009). For each individual I collected latex from three mature, sun-exposed leaves that were the youngest mature leaf on their branch. While still attached to the tree, leaves were cut transversally 1 cm from the tip, perpendicular to the midrib. For leaves with narrow, elongate (e.g. acuminate) tips, I cut 1 cm from the base of the narrow tip toward the leaf petiole. Following Rasmann *et al.* (2009), latex that was exuded from the cut was collected onto pre-weighed strips of filter paper. Latex was collected until it stopped flowing, which in most cases happened within 10 s. Paper strips with latex were placed into pre-weighed microcentrifuge tubes which were then re-weighed to obtain the fresh weight of latex exuded. I standardized latex exudation by the width of the transverse cut because different leaf morphologies led to widely different widths of cuts. Thus my measure of latex exudation is in units of mg mm^{-1} and is a metric of how much latex is exuded relative to leaf width.

Statistical analyses

I tested hypotheses about 1) the diversity of traits among co-occurring species, 2) the diversity of traits among co-occurring individuals, and 3) environments associated with variation in trait diversity.

Ficus *assemblages generated under null models*

The general strategy to testing co-occurrence hypotheses was to construct null *Ficus* assemblages independent of variation in traits but dependent on dispersal limitation.

Observed trait distributions among co-occuring trees were compared to trait diversity from null assemblages. I standardized observed quadrat trait metrics according to the distribution of metrics from null assemblages in that quadrat (Webb *et al.* 2002). Each observed quadrat metric was standardized to a z-score by subtracting the mean metric from the 1000 null quadrat assemblages and dividing by the standard deviation of those null metrics (Kraft *et al.* 2008, Swenson & Enquist 2009).

I used permutation techniques of generating null assemblages that held constant the extent of each species' occurence across the plot (N quadrats) and the local species richness of assemblages (N species in each quadrat; Gotelli & Entsminger 2001). Species occurence and local richness are partly dependent on dispersal patterns and this null model helps to avoid incorrect rejection of null hypotheses due to dispersal generated trait patterns (Kembel 2009). I generated 1,000 null assemblages of plot quadrats for species-level analyses. Null assemblages were generated using the "vegan" package in R.

I also permuted trait data among individuals in order test the null hypothesis that trait diversity of co-occurring individuals was random. Recently, Paine *et al.* (2011) permuted trait data among all individuals in a forest plot to generate a null model for trait patterns among co-occurring individuals. However, species' occurrences were not maintained in their null model, allowing species to be distributed at more quadrats than observed and losing the signal of each species' dispersal limitation. I took a different approach, maintaining species occurrences and richness in quadrats. I used the method of Gotelli and Entsminger (2001) to permute quadrat species occurrences and then permuted individual trait values within species. I attempted to maintain the total number

of individuals across species in a quadrat, because dispersal limitation could affect individual density. However, I was unable to constrain the number of species and individuals in all quadrats. I allowed variation in the total number of individuals across species in a quadrat, limited to within two individuals of observed. Additionally, in individual analyses I used trait metrics that conrolled for the number of individuals, thus avoiding bias toward greater trait diversity in quadrats with more individuals (Paine *et al.* 2011). I generated 1,000 null assemblages of plot quadrats for individual-level analyses.

Trait metrics

I used four metrics to characterize trait diversity of co-occurring *Ficus* to look for evidence of niche assembly: Trait Diversity (TD, Petchey & Gaston 2002), variance, standard deviation of nearest neighbor (SDNN), and SDNN standardized to trait range (SDNNr, Kraft & Ackerly 2010). High TD and trait variance are considered evidence for local niche differentiation and limiting similarity. Low TD and trait variance are considered evidence for spatial niche differentiation and environmental filtering. TD in quadrats was measured along a dendrogram of species trait values as the sum of branch lengths in the dendrogram shared by species in the quadrat divided by the sum of total dendrogram branch lengths (Petchey & Gaston 2002, Swenson & Enquist 2009). TD was computed using the "vegan" package in R. TD was only computed for species-level analyses and not for individual-level analyses because TD does not correct for the number of observations. Trait variance was calculated as the sum of squared trait deviations in a quadrat / (n – 1). SDNN is a measure of evenness in spacing of co-

occurring trees along a trait axis. Low SDNN means co-occurring trees are evenly spaced, which is considered evidence for local niche differentiation and limiting similarity (Kraft *et al.* 2010). SDNN was calculated by taking the distance in trait space between each species or individual and its nearest neighbor in trait space within the quadrat, and taking the standard deviation of those nearest neighbor distances. SDNN may be biased by the range of traits in a quadrat, *i.e.* quadrats with a larger range may have high magnitude trait variation and be biased toward high SDNN. Thus I used a fourth metric that standardizes SDNN by quadrat trait range (SDNNr, Kraft & Ackerly 2010).

Testing trait and environmental patterns

I tested diversity metrics of each of the six traits among co-occurring species and of the three leaf traits among co-occurring individuals. I tested trait diversity metrics of species and individuals co-occurring in 100, 400, and 2500 m^2 square quadrats. Individual-level SDNN and SDNNr were not tested in 100 m^2 quadrats because there were too few quadrats with at least 3 individuals (minimum required to calculate SDNN) at this scale. Additional scales were not tested due to data limitations. I excluded trees found in quadrats containing young successional stands of broad-leaf forest on ridges that are recovering from agricultural use, characterized by *Castanopsis cuspidata* (Fagaceae), because these stands may exhibit strong assembly differences compared to mature stands on the plot (Ding *et al.* 2011).

Null hypotheses about the distribution of standardized trait (z-scores) metrics

were tested using sign tests. The null hypothesis for the sign test was that trait metrics are distributed evenly about zero, which is the expected distribution under null assembly models. I used sign-tests because z-scores were sometimes not distributed symmetrically (a condition for more informative tests). Variation in trait distribution z-scores were tested for correlation with environmental variation. I calculated average conditions of the 3 topographic variables across each quadrat. I then compared quadrat environmental values to TD and trait variance z-scores using non-parametric Spearman's rank correlations. I focused on TD and trait variance correlations to environment because these were designed to test for environmental filtering. For each trait-metric combination I report the environmental variable with the strongest correlation among the spatial scales tested in order to focus on the strongest pattern for each trait.

RESULTS

Trait diversity of co-occurring species

Trait metrics exhibited stronger patterns at the two smaller spatial scales (100 and 400 m^2 quadrats) relative to the largest spatial scale (2500 m^2). Traits were both clustered and over-dispersed among co-occurring species depending on the trait-metric combination (Figure 3.2). Some traits exhibited evidence for both patterns. For example, SLA among co-occurring species had significantly lower variance than expected but also had significantly lower SDNN than expected (both metrics significant for all scales, sign test, $\alpha = 0.05$). Low variance indicates trait clustering while low SDNN indicates regularity in

the trait separation of co-occurring species (*i.e.* limiting similarity). Among traits, SLA also had the most significant patterns across metrics. The distribution of latex exudation among co-occurring species showed a similar pattern whereby trait diversity and variance indicated clustering and SDNN indicated limiting similarity. Leaf area was the only trait that showed significantly greater SDNN and SDNNr than expected (both metrics significant in 400 m^2 quadrats, sign test, $\alpha = 0.05$). Trait diversity patterns were distinct even between the two most highly correlated traits, SLA and maximum DBH (Spearman's $\rho = -0.81$, Figure 3.2).

Topographical patterns – Across traits, the strongest topographical correlates of TD and variance were almost always elevation. The strongest correlation for four of the six traits was one where traits were significantly less diverse at higher elevations, while one trait (leaf area) was significantly less diverse at lower elevations (Table 3.4; Spearman's rank correlation, $\alpha = 0.05$). The strongest topographical correlates of TD or variance occurred in the smallest quadrats (100 m^2) for five of six traits.

Trait diversity of co-occurring individuals

Intraspecific variation independent of interspecific variation was substantial (individual variation unexplained by species means: leaf area 10%, SLA 73%, succulence 58%). However, interspecific variation was significant for all three leaf traits sampled among individuals ≥ 10 cm DBH (Kruskal-Wallis rank sum test, $p<10^{-16}$ for all three traits).

In general I observed stronger trait signal among co-occurring individuals ≥ 10 cm DBH compared to species-level analyses conducted on the same trees (Figure 3.3).

All three leaf traits exhibited significantly less variance among co-occurring individuals than expected under the null model (sign test, $\alpha = 0.05$). Leaf succulence showed the strongest evidence for limiting similarity among co-occurring individuals, having significantly lower SDNN at all scales than expected under the null model. Highly significant trait patterns mostly occurred at the scale of 100 and 400 m^2 quadrats, though this trend was weaker for individual-level analyses compared to species-level analyses (e.g. leaf succulence, Figure 3.3).

Topographical patterns – Each topographical variable was the strongest correlate of variance for a single leaf trait. Only leaf succulence and area had significant correlations between standardized trait variance and a topographical variable; no SLA patterns were significant (Table 3.4; Spearman's rank correlation, $\alpha = 0.05$). The strongest topographical correlations occurred at three different quadrat sizes for the three traits.

DISCUSSION

Individual-level variation in functional traits and niches may mediate the role of niche differentiation in spatial community variation. *Ficus* is a model of global tree diversity in lowland tropical forests, though the role of niche differentiation in the diversity of *Ficus* assemblages has not been well studied. I found evidence that multiple niche axes affect co-occurrence of *Ficus* species. Metrics indicated evidence for niche mechanisms with opposing effects on trait distributions, suggesting that both spatial niche differentiation across environments and local niche differentiation affect *Ficus* distributions across the

study site (Swenson & Enquist 2009, Kraft & Ackerly 2010). Across trait metrics, non-random co-occurrence patterns were strongest at small spatial scales, agreeing with previous studies of co-occurrence in tropical forest plots (Swenson & Enquist 2009, Kraft & Ackerly 2010). A previous study my study forest plot found that tree species distributions were spatially random for larger size classes, potentially indicating a limited assembly role for niche differentiation along spatial environmental gradients (Lan *et al.* 2009). However, another study at the plot identified many species distributions, including at large size-classes, that were best predicted by environmental variables (Hu *et al.* 2011). I found strong evidence for spatial niche differentiation among the most diverse genus on the plot.

In general, the strongest topographical correlate of TD and trait variance was elevation. The negative elevation-trait diversity correlations observed suggest stronger spatial niche differentiation at higher elevations, possibly due to moisture limitations. Seasonal drought has physiological effects on trees at Xishuangbanna, as evidenced by partial deciduous habits of some species in the dry season (Zhang & Cao 1995). Forests in Xishuangbanna have a strong dry season (5 months below 30 mm precipitation, Zhang & Cao 1995). Dry season drought was a major factor affecting interspecific variation in seedling survival and species distributions across scales in lowland Panamanian forest (Engelbrecht *et al.* 2005, Engelbrecht *et al*. 2007). Soil moisture in my study plot was likely greatest and drought stress lowest at the lowest elevations, in the beds of intermittent streams (Daws *et al.* 2002). Abiotic limitations can be more important to community assembly in harsh environments than in benign environments (Chase 2007),

which would be consistent with low soil moisture causing greater spatial niche differentiation at higher elevations. On the contrary, facilitation by species with diverse traits in harsh environments could generate high trait diversity in harsh environments (Spasojevic & Suding 2011). I observed greater trait diversity at high elevations for one trait, leaf area, and species with diverse leaf areas might facilitate each other under drier conditions. Soil properties may also affect niche assembly processes (Katabuchi *et al.* 2012), though I did not address those here.

Individual trait variance was most strongly related to elevation for only leaf succulence. However, soil moisture may have been the cause of low leaf succulence variance at higher elevations and low SLA variance in convex quadrats (Table 3.4). Like higher elevations in my study plot, convex quadrats (ridges) are also expected to be relatively dry (Daws *et al.* 2002). For diverse biomes, interspecific (Cunningham *et al.* 1999, Cornwell & Ackerly 2009) and intraspecific (van Hees 1997, Cornwell & Ackerly 2009) patterns find low SLA associated with low moisture and precipitation. Intraspecific variation in SLA is also affected by light environment, although my focus on larger individuals for intraspecific analyses likely reduced some of the high SLA variability associated with leaves in low light environments (Long *et al.* 2011). If soil moisture is a major driver of tree distributions in Xishuangbanna, these tree communities may be highly sensitive to fragmentation. Previous research found significantly lower soil moisture inside forest fragments in the regions compared to larger tracts (Zhu *et al.* 2004) and the situation may be exacerbated by the rapid expansion of water inefficient rubber plantations (*Hevea brasiliensis*, Euphorbiaceae; Tan *et al.* 2011).

Ficus trait variation associated with drought tolerance may correspond to life history variation. Hemi-epiphytic *Ficus* species tend to have a suite of characteristics associated with drought tolerance, and I found that all hemi-epiphytes had lower SLA than other species (Tables 3.1 and 3.2, all species with 3 or fewer individuals on the plot, except for *F. vasculosa*, are hemi-epiphytes, Hao *et al.* 2011). However, hemi-epiphytes were rare in my study site, as is typical for these dispersal limited species (Laman 1996). Thus hemi-epiphytes likely played a relatively weak role in driving the patterns I observed, which were likely driven by more abundant species (Harrison 2005).

Individual-level analyses of trait distributions detected more non-random patterns among co-occurring trees compared to analyses using species mean trait values (Paine *et al.* 2011). Many of the significant trait patterns among co-occurring individuals were also significant among species, but more weakly so. There were no sign changes in significant relationships between species and individual-level analyses, indicating that species-level analyses would not come to opposite conclusions about the relative importance of the two kinds of niche assembly considered. However, trait diversity patterns may have limited ability to discern the relative importance of the niche axes because of power differences among trait metrics (Kraft & Ackerly 2010).

I believe that my null model of individual tree assembly, which maintained the number of quadrats in which a species occurred, was appropriately more conservative than that used by Paine *et al.* (2011). However, the construction of appropriate permutation-based null models in spatial ecology is non-trivial because of the difficulty in maintaining autocorrelation common in spatial data and the ability of limited dispersal

to generate pattern in biodiversity (Kembel 2009, Guillot & Rousset 2011). The appropriateness of null permutation models for trait-based assembly studies on forest plots, where dispersal limitation plays an important role in species distributions (Hubbell *et al. 1*999), requires further investigation (Kraft & Ackerly 2010).

The increase in power with individual-level analyses varied across traits. For example, SLA variance was significantly low for all scales in individual analyses, like the other traits. Yet in species-level analyses on the same trees (Figure 3.3), leaf succulence and leaf area had significantly low variance at all scales, while SLA variance was significantly low only in 100 m^2 quadrats. Leaf succulence SDNN among individuals was significantly less than zero at all scales, although SDNN at the species level among the same trees was not significant. Species-level SLA and leaf succulence patterns may have been weakened by high intraspecific variation in these traits (73% of total SLA and 58% of total leaf succulence variation). Sampling of additional species not included in individual analyses revealed strong SLA patterns among co-occurring species (Figure 3.2). Thus individual-level sampling and increased number of species sampled increased power to detect evidence of niche effects.

Traits like SLA that vary greatly within species could be identified through pilot sampling. My results affirm that results based on species mean traits should be interpreted with caution, especially for traits with high intraspecific variability, and that a lack of significant trait signal may merely be due to the inaccurate assumption that individuals of the same species have identical traits and niches (Messier *et al.* 2010, Violle *et al.* 2011). SLA is often highly variable among individuals in plant communities.

In trait-based studies of co-occurrence, individual measurement of the most individually variable traits can be critical to detecting non-random trait patterns (Albert *et al.* 2011, Paine *et al.* 2011). In a floodplain grassland community in Luxembourg, SLA was the trait with the greatest intraspecific variation and the trait with the greatest change in distribution depending on whether data were analyzed at the species or individual level (Jung *et al.* 2010). SLA also was the most intraspecifically variable trait across British flora (Wilson *et al.* 1999) and Mediterranean shrublands (Garnier *et al.* 2001), but was not in some other communities (Albert *et al.* 2010).

A trait with high intraspecific variation such as SLA may correspond to weaker competition at the species level because species have high niche variances (MacArthur & Levin 1967, Bolnick *et al.* 2011). My results partially supported this hypothesis: among all species (Figure 3.2), SLA had significantly low variance across scales, which may be due to weak local niche differentiation, but SLA simultaneously had significantly low SDNN across scales, indicating potentially strong local niche differentiation. However, the *Ficus* species I studied were embedded in a much larger competitive community and thus unobserved SLA patterns in additional species likely played a role in these patterns. Most of the increased power to detect trait patterns was at a large scales (2500 m^2 quadrats), which had fewer numbers of quadrats sampled and showed weak trait patterns in previous research (Swenson & Enquist 2009). The change in power across scales may largely depend on the scale of sampling relative to the scale at which niche processes differentiate and the number of sites sampled, which is fewer at larger scales.

At least three distinct mechanisms could generate signals of niche-based

assembly among individuals (Jung *et al.* 2010). First, local abiotic conditions and neighborhood competition may select among individuals based on their phenotype (*i.e*. environmental filtering or limiting similarity). Second, individuals of multiple species may plastically match their phenotype to the abiotic and biotic environment in a correlated or repelling manner, without any environmental selection among phenotypes (Rausher 1992). However, highly correlated plastic responses across species may arise due to environmental selection. It is unknown how important plastic responses that are correlated across species are for individual trait patterns (Cornwell & Ackerly 2009, Jung *et al.* 2010, Paine *et al.* 2011). Third, a mechanism not noted in previous studies (Cornwell & Ackerly 2009, Jung *et al.* 2010, Paine *et al.* 2011) is that trait similarity of co-occurring individuals of the same species could be neutral and simply caused by limited dispersal and relatedness. These last two explanations merit further investigation before strong conclusions can be generated from individual-level trait studies.

My study is one of the first to study how a trait directly involved in herbivore defense mediates tree species coexistence (Cingolani *et al.* 2007 and Paine *et al.* 2011 studied leaf toughness). Neither of the previous studies reported results on trait diversity of leaf toughness, though Cingoliana *et al.* (2007) noted that average species leaf toughness in Argentine grasslands decreased with increasing moisture and decreased grazing. I expected that a trait involved in biotic interactions would be more likely to show over-dispersion among co-occurring species (Webb *et al*. 2002), however I found limited evidence for this pattern along an axis of variation in latex exudation. I observed significantly low SDNN of latex exudation in 100 m^2 quadrats, indicating even spacing

of co-occurring species along an axis of latex production. However, I also observed low TD and variance in latex exudation among co-occurring species in 100 and 400 m^2 quadrats. Potential effects of latex and herbivore defense strategy on coexistence may have been outweighed by assembly processes along other trait axes. I may have had limited power to detect latex effects with a sample of 18 species. Additionally, interspecific variation in the amount of latex produced by *Ficus* species may have effects of small magnitude on palatibility to herbivores, though little research has been conducted on this topic (one generalist weevil, *Oribius* sp., tested in Basset & Novotny 1999).

Large scale environmental, evolutionary, and dispersal processes may have influenced patterns I observed in this study. Xishuangbanna occurs near the northern range limit of dipterocarp rainforests. Nearly all of the study species are near their northern range limit in Xishuangbanna, though they are found across large areas to the south (e.g. Sundaland; Wu *et al.* 2003). Abiotic limitations may be more important to limiting species distributions near their poleward range boundaries as opposed to at tropical boundaries (Wiens 2011). Whether abiotic limitations near poleward range boundaries also are more important drivers of small scale distributions across a forest plot merits further exploration. Additionally, the distribution of environmental conditions across Southeast Asia and the evolutionary history of *Ficus* can affect on whether species specialize to environmental conditions varying within my plot (Brown & Pavlovic 1992). These large scale forces affect the *Ficus* species pool and may limit my ability to observe assembly processes (Ricklefs 1987, Hugueny *et al.* 1997).

Conclusions

Individual variation is important to consider in trait-based studies of assembly, especially for traits with high intraspecific variation. I detected more non-random patterns of trait diversity among co-occurring individuals than species, suggesting niche assembly axes may be better revealed when accounting for intraspecific variation. However, intraspecific trait diversity patterns were weakly correlated to topographical variation, while higher elevation was strongly related to a decrease in diversity of most species-level traits, suggesting an axis of spatial niche differentiation. My study suggests potential niche axes whereby *Ficus* species can coexist, which has been one of the most well-studied genera of tropical trees, though their non-reproductive ecology has been less well studied. Previous authors have noted and sought explanations for the high species richness of *Ficus* assemblages but had not examined in detail how they contribute to patterns of co-occurrence on a forest plot (Janzen 1979, Herre 1989, Thornton *et al.* 1996, Harrison *et al.* 2003, Harrison 2005, Harrison & Shanahan 2005). The importance of interspecific interactions among *Ficus* species in generating these patterns is unclear because many other species coexist and compete with the study *Ficus* species. However, *Ficus* is the most speciose genus on my study plot. My results suggest that that niche partitioning across environments and within environments may contribute to their coexistence.

Tables

Table 3.1. The abundance, total basal area, and number of individuals sampled of *Ficus* species. Species are ranked by total number of individuals on the plot.

Species	Individuals on plot (N)	Total basal area on plot (m^2)	Individuals on plot DBH ≥ 10 cm (N)	Individuals sampled DBH ≥ 10 cm (n)	Individuals sampled from plot and garden (n)
F. langkokensis	1350	7.81	277	199	209
F. fistulosa	780	0.54	3	0	7
F. sp. 1	210	0.9	20	13	15
F. chrysocarpa	184	0.44	13	12	14
F. auriculata	115	1.64	55	43	44
F. hispida	68	0.07	0	0	9
F. esquiroliana	67	0.84	24	6	10
F. variolosa	57	2.08	26	2	5
F. hirta	55	0.01	0	0	5
F. oligodon	54	0.69	27	22	24
F. glaberrima	41	0.63	12	9	10
F. semicordata	39	1.62	37	25	26
F. sp. 3	33	0.15	2	0	0
F. subincisa	23	0.01	0	0	5
F. sp. 2	13	9.49	6	2	2
F. cyrtophylla	6	0.02	1	1	5
F. altissima	3	4.46	3	0	5
F. benjamina	2	3.85	2	0	5
F. lacor	2	2.09	2	1	5
F. stricta	2	1.94	2	0	4
F. sagittata	1	0.01	1	0	0
F. vasculosa	1	0.02	1	0	5

Table 3.2. Species trait values for the six functional traits tested. Values used in species-level analyses are shown. **Ficus subincisa* exuded a vanishingly small amount of latex that I was unable to measure.

Species	Maximum DBH (cm)	Syconium diameter (cm)	Latex exudation (mg mm^{-1})	Leaf succulence (mg cm^{-2})	SLA (cm^2 g^{-1})	Leaf area (cm^2)
F. altissima	2277.1	2.3	0.48	24.3	72.6	187.1
F. auriculata	293.8	4.5	0.10	17.4	148.8	455.8
F. benjamina	2159.2	1.4	0.06	13.7	136.4	23.5
F. chrysocarpa	223.1	1.3	0.08	15.2	195.8	281.2
F. cyrtophylla	124.2	9.0	0.08	9.4	291.1	114.8
F. esquiroliana	414.0	2.1	0.05	13.9	194.1	510.2
F. fistulosa	118.2	1.9	0.02	15.5	206.6	135.3
F. glaberrima	653.8	0.9	0.02	11.6	158.4	60.8
F. hirta	46.0	2.3	0.07	10.6	360.5	86.3
F. hispida	90.1	2.1	0.05	11.2	219.3	154.1
F. langkokensis	352.3	0.9	0.02	10.0	216.3	52.0
F. lacor	1560.5	1.0	0.08	14.0	123.1	105.1
F. oligodon	370.1	2.8	0.12	13.7	166.0	188.9
F. sagittata	121.0	1.2	*n/a*	*n/a*	*n/a*	*n/a*
F. semicordata	349.7	1.3	0.07	12.7	186.3	130.9
F. stricta	1528.7	1.7	0.24	21.1	81.3	39.4
F. subincisa	72.0	1.6	*0.00	9.3	210.9	44.9
F. variolosa	745.2	1.1	0.04	14.8	185.3	113.4
F. vasculosa	158.0	0.9	0.05	15.2	144.7	43.6
F. sp. 1	393.6	*n/a*	*n/a*	18.6	178.3	120.2
F. sp. 2	2547.8	*n/a*	*n/a*	14.9	126.3	171.5
F. sp. 3	340.8	*n/a*	*n/a*	*n/a*	*n/a*	*n/a*

Table 3.3. Non-parametric rank-correlation among functional traits used in analyses (Spearman's ρ).

	Syconium diameter	Latex exudation	Leaf succulence	SLA	Leaf area
Maximum DBH	-0.24	0.37	0.46	-0.81	-0.09
Syconium diameter		0.53	0.03	0.21	0.52
Latex exudation			0.50	-0.47	0.35
Leaf succulence				-0.72	0.23
SLA					0.15

Table 3.4. Topographic variables most strongly related to measures of trait diversity for each trait. Both species and individual-level results are shown. Note that trait diversity and variance were tested for species-level analyses, while only variance was only tested for individual-level analyses. Correlations use Spearman's non-parametric rank correlation.

	Trait	Quadrat size (m^2)	Topographic variable	Trait metric	Spearman's ρ	p
Species-level analysis	Maximum DBH	400	Concavity	Trait diversity	-0.16	0.0102
	Syconium diameter	100	Elevation	Trait diversity	-0.15	0.0054
	Latex exudation	100	Elevation	Variance	-0.20	0.0002
	Leaf succulence	100	Elevation	Trait diversity	-0.21	< 0.0001
	SLA	100	Elevation	Trait diversity	-0.14	0.0043
	Leaf area	100	Elevation	Trait diversity	0.18	0.0002
Individual-level analysis	Leaf succulence	400	Elevation	Variance	-0.28	0.0107
	SLA	2500	Concavity	Variance	-0.17	0.2606
	Leaf area	100	Slope	Variance	0.30	0.0148

Figures

Figure 3.1. Map of the Xishuangbanna 20-ha plot showing *Ficus* individuals and those large trees (DBH ≥ 10 cm) whose leaf traits were sampled. Younger secondary forests excluded from individual samples and from all analyses were found on ridge-tops. DBH is indicated via circle size on a log scale.

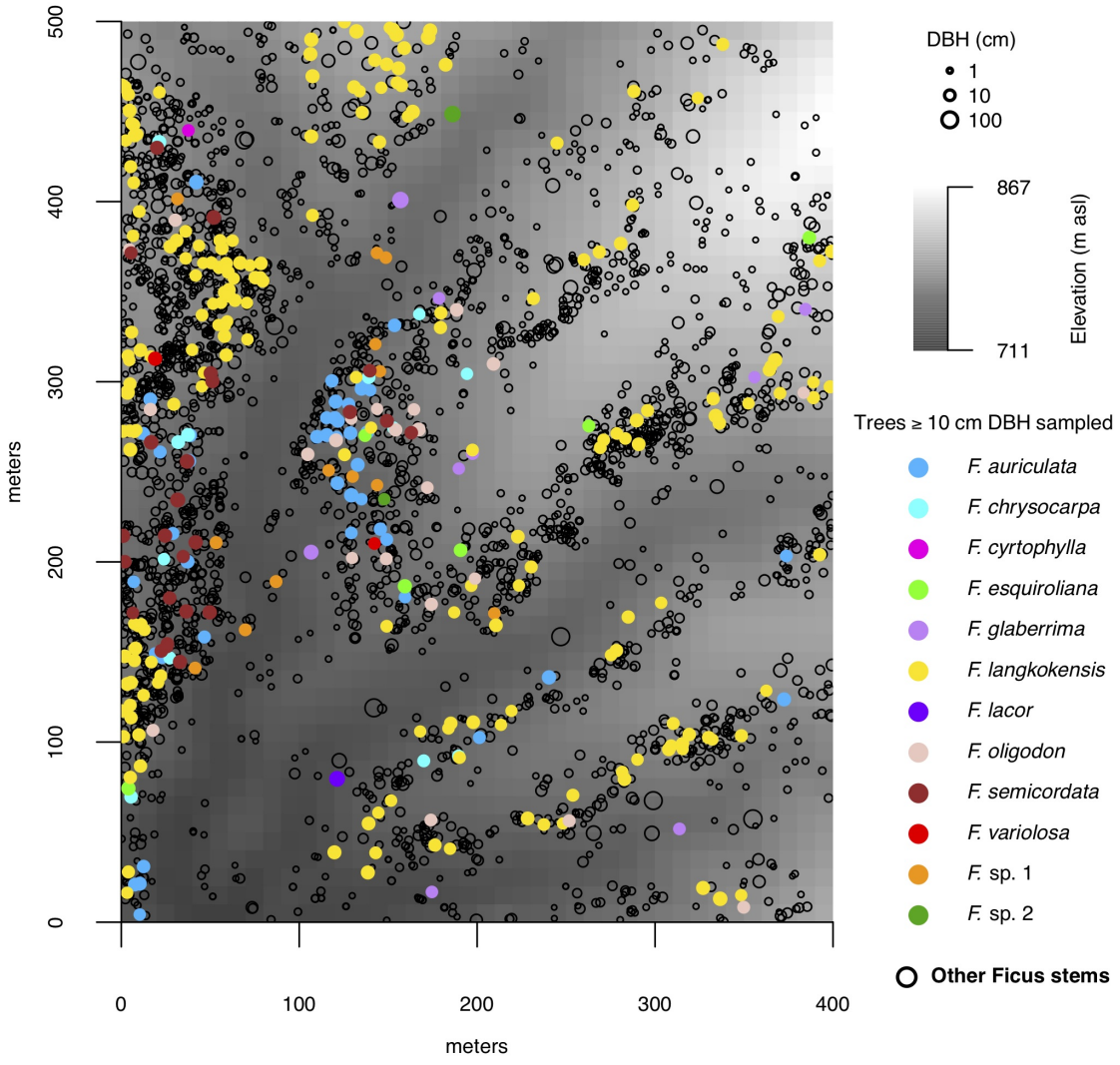


Figure 3.2. Trait distributions of co-occurring species relative to null assemblages (permutations). The median and 95% CI of the median quadrat Z-score are shown for each trait-metric-scale combination. The significance of sign tests on Z-score distributions are indicated as: "." $0.1 > p > 0.05$, "*" $0.05 > p > 0.005$, "**" $0.005 > p > 0.0005$, "***" $0.0005 > p$. A conservative Bonferroni α for the species-level tests shown below would be $0.05 / 72 = 0.0007$ ("***" tests are significant under this criterion).

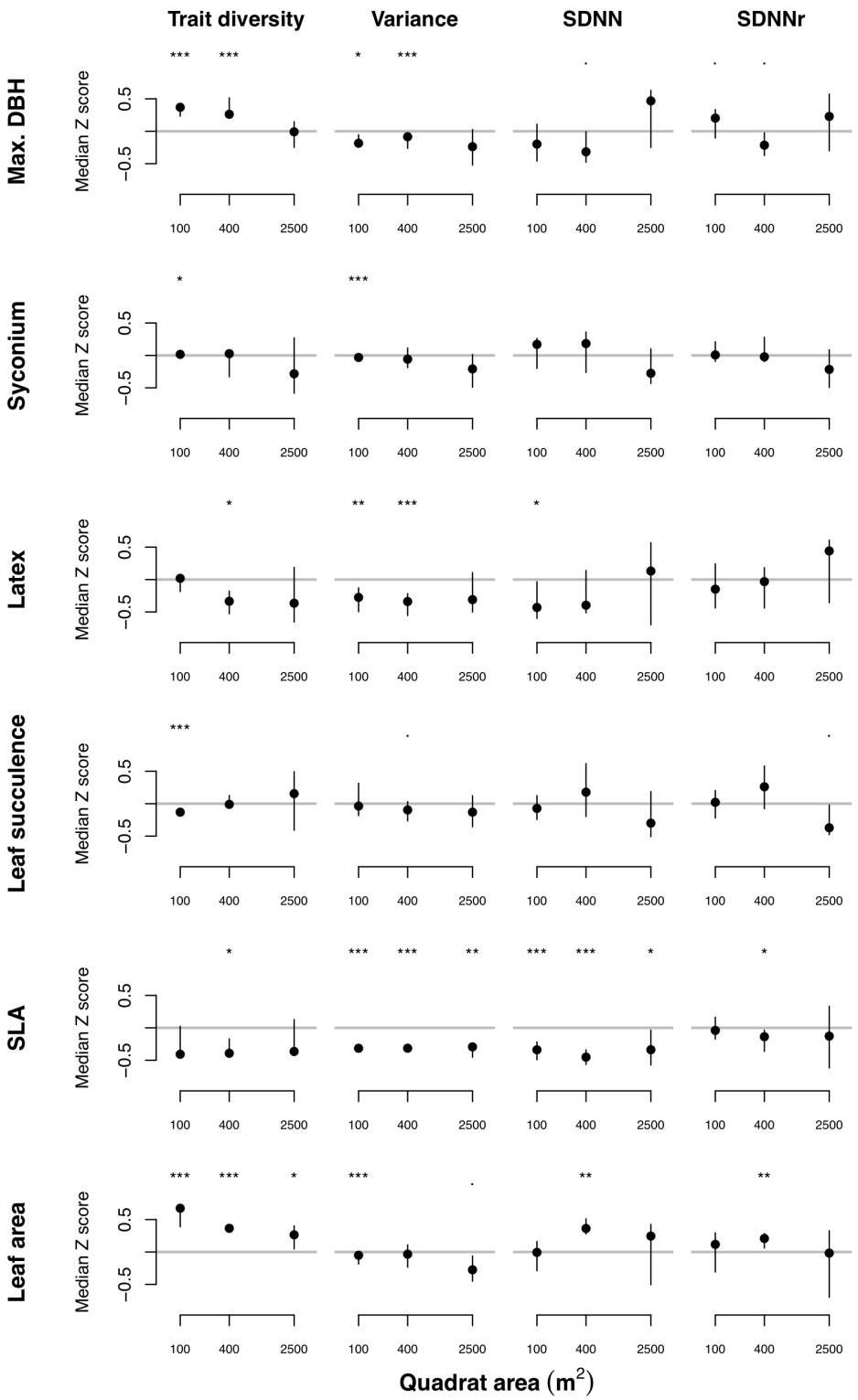
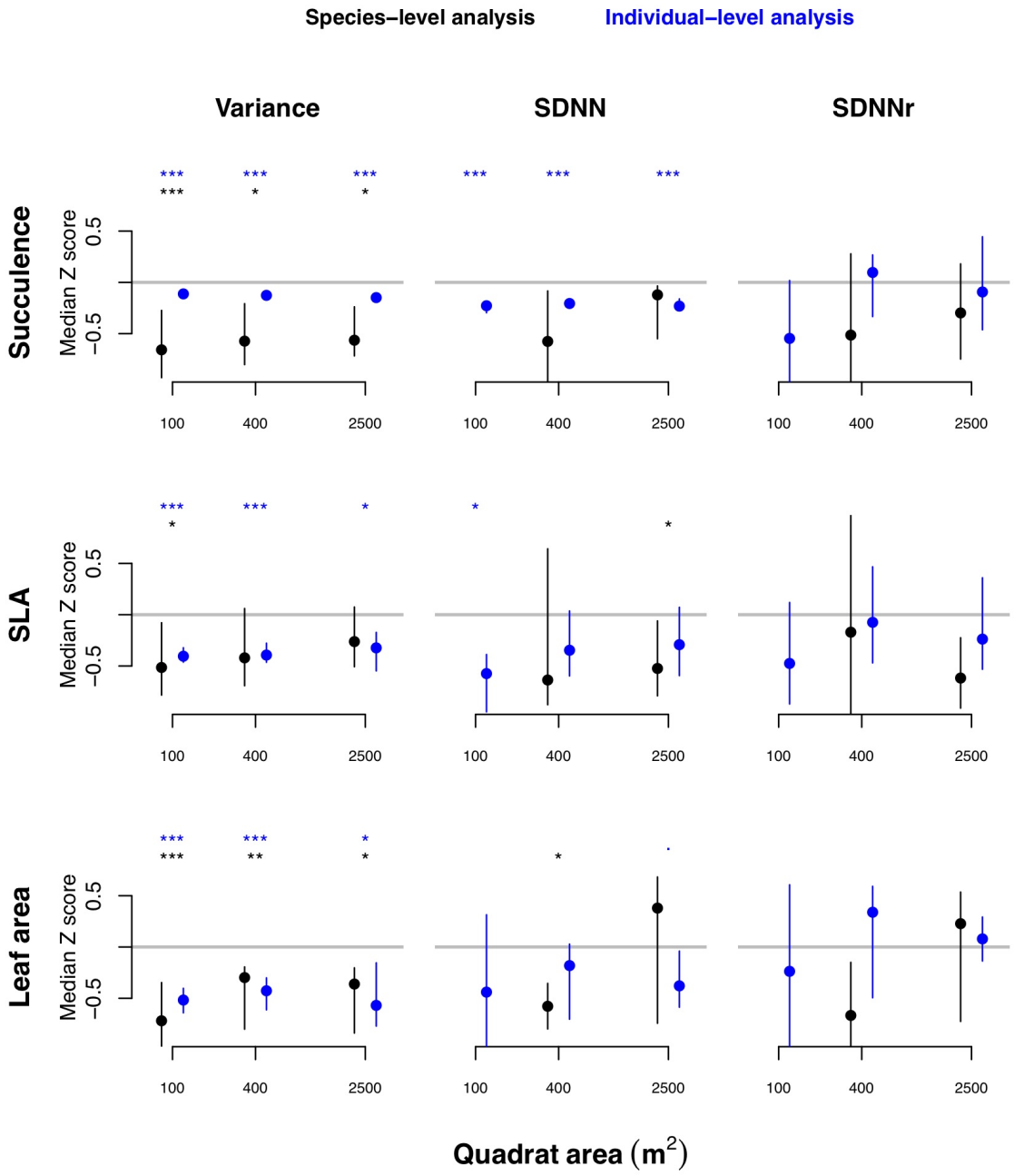

Trait diversity
Variance
SDNN
SDNNr
Max. DBH
Syconium
Latex
Leaf succulence
SLA
Leaf area
Median Z score
0.5
−0.5
100
400
2500
Quadrat area (m2)

Figure 3.3. Trait distributions of co-occurring individuals and species relative to null assemblages (permutations). Species-level analyses were done on trees from the individual-level analysis in order to compare results. The median and 95% CI of the median quadrat Z-score are shown for each trait-metric-scale combination. The significance of sign tests on Z-score distributions are indicated as: "." $0.1 > p > 0.05$, "*" $0.05 > p > 0.005$, "**" $0.005 > p > 0.0005$, "***" $0.0005 > p$. A conservative Bonferroni α for the species-level or individual-level tests shown below would be $0.05 / 27 = 0.002$ ("**" tests are significant under this criterion).


Species–level analysis
Individual–level analysis
Variance
SDNN
SDNNr
Succulence
SLA
Leaf area
Median Z score
0.5
−0.5
100
400
2500
Quadrat area (m²)

Chapter IV

Tree community dynamics: effects of environmental selection along trait axes

INTRODUCTION

Researchers are increasingly using the trait patterns of co-occurring species to test for the presence of niche processes (Legendre *et al.* 1997, Kraft *et al.* 2008, Swenson & Enquist 2009, Lebrija-Trejos *et al.* 2010). Co-occurrence of species with similar traits (*i.e.* trait clustering or under-dispersion), such as when sclerophyllous species co-occur in xeric habitat, is considered evidence that species niches are largely separated in space along environmental gradients and communities are assembled by environmental filtering (Keddy 1992, Cavender-Bares *et al.* 2004). Niche models based on trait-based environmental selective filters may be more accurate and flexible predictive models of community dynamics compared to traditional approaches (Webb *et al.* 2010).

Traditional approaches that quantify species replacement along environmental gradients are limited because it is difficult to determine if species are present because of favorable conditions or because of dispersal patterns (Legendre *et al.* 1997, Kraft *et al.* 2008, Swenson & Enquist 2009, Lebrija-Trejos *et al.* 2010). Both dispersal and spatially

autocorrelated environments can generate spatial community turnover, however their independent effects are obscured because dispersal data are rarely available. Additionally, dispersal can mask true niche relationships, as is the case in sink populations (Pulliam 1988). An indirect method to estimate dispersal patterns is to use permutations of species by site occurrences as a model of dispersal history (e.g. Gotelli & Entsminger 2001). However, it is unclear how accurately permutation models represent dispersal assembly on forest plots (Kembel 2009). Rather than interpreting occurrence or abundance patterns along gradients as indicating optimal conditions for species, a more powerful approach is to analyze longitudinal measurements of individual performance in different environments (Davies 2001, Uriarte *et al.* 2010). By tracking individual performance through time, the confounding influence of dispersal is eliminated and thus allows for a more direct determination of niche effects.

Spatial variation in performance among individual trees may reveal spatial niche differentiation that is undetected when studying larger scale, plot-level dynamics (Huston 1999, Clark *et al.* 2010) though some traditional trait approaches ignore individual-level demographic patterns (e.g. Legendre *et al.* 1997). The analysis of individual dynamics is an emerging frontier in community ecology due to increasing efforts to collect long term, large scale data and advancing computational methods (Condit *et al.* 2006, Russo *et al.* 2008, Clark 2010, Uriarte *et al. In press*). Previous investigators of environmental effects on tree demographics have focused on the effect of biotic neighborhood (Uriarte *et al.* 2004, Uriarte *et al.* 2010) and the effects of different soil types on demographic trade-offs (Davies 2001, Russo *et al.* 2008). Demographic trade-offs across environmental

gradients occur when species having greater relative growth in one environment have greater relative survival in a different environment (Russo *et al.* 2008). Such trade-offs can underlie spatial niche partitioning among environments (Kobe 1996). Investigators have not yet estimated spatial variation in environmental selection functions that may drive spatial niche differentiation at the plot scale.

The concept of environmental filtering in community ecology (Weiher & Keddy 1995, Webb *et al.* 2010) is analogous to that of spatial gradients in natural selection on intraspecific trait variation, a topic with a long history of research in evolutionary biology. A fitness landscape is the function describing the change in individual fitness across variation in phenotype (Wright 1932). Haldane (1954) proposed estimating the selection on a trait by quantifying the difference in relative fitness across trait variation, which I extend to trait variation among species. The fitness landscape, or selection function, can change across environments, creating a selective gradient. Selective gradients are often quantified in observational data that test how the fitness-phenotype correlation changes across environments (Kalisz 1986). Spatial environmental niche differentiation among species may be similarly inferred from changes in the trait-fitness relationship across environments. Covariance between the selection function and local environment are evidence that the environmental gradient may be the cause of variation in selection (Wade & Kalisz 1990). From a community perspective, I aim to characterize the role of environmental selection on community spatial variation, which is analogous to quantifying the variation in trait-based selective gradients across environments.

The primary objectives of this study are 1) to quantify environmental selection

effects on communities and 2) to determine which environmental and trait axes exhibit the strongest selection. I quantify environmental filtering using a novel combination of techniques that synthesizes advances of recent studies (Clark *et al.* 2010, Kraft & Ackerly 2010, Uriarte *et al.* 2010). First, I study individual tree dynamics to infer environmental selection, which eliminates dispersal as a confounding factor. Second, I simplify spatial variation in performance by considering performance a function of trait values and trait differences, which are proxies for niche variation. Approaches to studying environmental tropical tree community assembly that do not account for functional variation have found limited importance for environment (Harms *et al.* 2004, Valencia *et al.* 2004), while my functional trait approach may be more powerful by incorporating this additional information. Results from trait-based research have more relevance to additional systems than species-specific results, and may suggest underlying ecophysiological mechanisms (McGill *et al.* 2006, Webb *et al.* 2010). Furthermore, trait-based community predictions may be better applied to large scales because ideally they are relatively context-independent, which is necessary for prediction of impacts of land-use on communities (Dale & Rauscher 1994). Third, I model all species simultaneously to account for rare species that comprise much of species richness. Many previous studies of trait-based community dynamics have been limited to a handful of abundant species (Davies 2001, Uriarte *et al.* 2010). Finally, I employ hierarchical Bayes models, which simplify high-dimensional uncertainty through hierarchical organization and provide a flexible framework for further model development (Clark 2005, Clark & Gelfand 2006).

I use this approach to assess which environmental performance filters are most important in community-wide growth and mortality. I also determine which filters show the greatest spatial variation that may thus be most important for species co-existence on the plot. I assess how filters change between survival and growth in order to characterize life history trade-offs and their spatial variation.

METHODS

Study site

I studied changes in the tree community at the 25-ha Fushan Forest Dynamics Plot (FDP) in northern Taiwan (24°45'40"N, 121°33'28"E, 615-730 m asl). Fushan FDP was established in 2003 following Center for Tropical Forest Science (CTFS) protocols in which all trees with diameter at breast height (DBH, at 1.3 m height) ≥ 1cm were mapped, tagged, identified, and measured by I-Fang Sun and collaborators (Condit 1998). The forest at the site is a subtropical evergreen broad-leaved forest receiving 4,271 mm yr^{-1} rain. The soils are extremely acidic (pH ~3.3-4.3) with low organic carbon content and fertility (Su *et al.* 2007). A detailed description of the plot can be found in Su *et al.* (2007). I studied dynamics of stems first recorded in a 2003 census and then re-censused in 2008. I did not model the dynamics of three species of *Cyathea* tree ferns (Cyatheaceae) because their growth involves little radial trunk expansion, which is the growth measured by change in DBH. Excluding tree ferns, a total of 163,400 stems and 111,593 individuals of 107 species were recorded in 2003, with 132,426 stems and

95,436 individuals surviving to 2008. I divided the plot into 625 square quadrats with 20 m edges (quadrat area = 400 m^2). This scale offers a reasonable trade-off between sample sizes at two levels: 1) number of trees within quadrats, required to model local environmental selection, and 2) number of quadrats within the plot, required to model spatial heterogeneity of selection (Swenson & Enquist 2009, Kraft & Ackerly 2010).

I focused on two topographic attributes of 20 x 20 m quadrats: convexity and slope. Following Harms *et al.* (2001) and Valencia *et al.* (2004), elevation of a quadrat was defined as the mean elevation values at its four corners. Convexity was the elevation of a quadrat minus the mean elevation of the eight surrounding quadrats. Slope was the mean angular deviation from horizontal of each of the four triangular planes formed by connecting three corners of a quadrat.

Topographical gradients are often highly correlated to variation in soil moisture in tropical forests (Daws *et al.* 2002). Variation in soil moisture and soil nutrients can have strong impacts on tree demography and forest communities within plots (Engelbrecht *et al.* 2007, John *et al.* 2007). Previous analyses of the Fushan forest have suggested topographical concavity is associated with interspecific variation in survival (I-Fang Sun, *unpublished data*). Subtropical rainforests in Taiwan are thought to be highly P-limited (Wu *et al.* 2007). Tropical forests are also strongly N-limited, especially in young soils such as those in Taiwan (Taiwan is ~3 million years old; Lebauer & Treseder 2008).

Soil samples were collected from 80 cells that ranged from 40x40 m to 100x80m. Four soil samples were collected from each cell and were mixed together for chemical analysis. Geostatistic software (Surfer 7.0) was used to produce the soil distribution map

for the plot, and then kriging was used to estimate soil properties for each 20x20m quadrat. Soil pH was measured using a mixture of soil and deionized water (1:1, w/v) with a glass electrode (McLean 1982); total organic carbon (OC) content was determined using the Walkley–Black wet oxidation method (Nelson & Sommers 1982); available N was extracted by 1 M KCl and measured withthe Kjeldhal method (Bremner & Keeney 1966). Available P was measured via the Bray No. 1 method (Kuo 1996).

Trait data

I-Fang Sun and others measured leaf traits on the six largest and the six smallest individuals of each tree species in the Fushan 25-ha plot. They collected three mature, sun-exposed leaves from each individual, and leaves were processed the evening they were collected (Cornelissen *et al.* 2003). For tree height, the six largest individuals of each species were selcted and the height to the highest leaves was measured for all individuals. Trees taller than 15m were measured with a laser range finder; for shorter trees a pole was used to measure their height. For wood density, five individuals of each species were randomly selected and had a wood sample collected with increment borers. Water displacement was used to measure fresh wood volume, then the wood samples were oven-dried to constant weight at 80°C. Wood density was calculated by dividing the dry weight over its wood volume. Average density of samples was taken where samples were weighted by their length.

I calculated leaf area, specific leaf area (SLA; leaf area / dry mass), and leaf succulence [(fresh mass – dry mass) / leaf area], because these traits have been

previously identified as potential axes of niche differentiation in subtropical and tropical forests (Swenson & Enquist 2009, Kraft & Ackerly 2010, Uriarte *et al.* 2010). Variation in these traits is thought to reveal life-history trade-offs and niche variation: (1) leaf area is subject to a trade-off between light capture and increased temperature (Dolph and Dilcher 1980), (2) SLA represents a trade-off between cost of leaf growth vs. photosynthetic rate (Wright *et al.* 2004), (3) leaf succulence is subject to a trade-off between high productivity vs. long leaf life span (Garnier & Laurent 1994), (4) wood density represents a trade-off between growth and survival (Mueller-Landau 2004), and (5) maximum height represents the light niche of adults (King *et al.* 2006). I obtained leaf trait data for a total of 99 species, maximum height data for 96 species, and wood density for 75 species (five of which came from the Global Wood Density Database; Chave *et al.* 2009, Zanne *et al.* 2009). However, traits do not vary independently and I calculated the first two principal components axes of leaf and maximum height trait data for the 96 species having these data (Table 4.1).

Models of trait-based environmental selection

I used a hierarchical Bayes approach to statistical inference primarily for the flexibility of such models, allowing me to integrate over many sources of uncertainty. Simultaneously modeling spatial variation in the performance of all species is a challenging high-dimensional problem because species vary in their intrinsic ontogeny and environmental selection varies in space. A hierarchical approach simplifies high-dimensional uncertainty and facilitates model convergence by constraining many parameters to hyper-

distributions (Clark 2005, Clark & Gelfand 2006), instead of estimating species-specific demographic parameters independently. The constraints of hyper-distributions allow inference about parameters for species for which few observations exist, allowing us to model the whole community.

In Bayesian inference, the posterior probability of parameters are estimated, defined as the probability of parameter values given the observed data. The posterior is proportional to the likelihood of the data given the parameters multiplied by the prior probability of the parameter values. I assumed essentially no prior information about the parameter values and gave diffuse distributions to priors, *i.e.* all parameter values have essentially equal probability. Below I present equations used to calculate the expected growth or survival given the parameters. The full likelihood function and conditional posterior probabilities are presented in the Appendix.

My model builds on the ontogenetic growth and survival functions of Uriarte *et al.* (2004) by adding in environmental selection and hierarchical organization of community-wide dynamics. The expected growth of an individual stem i of species s in quadrat q is

$$E(g_i) = \exp(g_s + \delta_i + F_{sq}) \qquad (1)$$

where g_s determines maximal growth of species s, δ_i is the reduction in growth of stem i due to its size, and F_{sq} is the reduction in growth due to environmental selection against the species in quadrat q. When the last two terms in the exponent equal zero they have no effect and the expected growth is the species maximum. Survival models are a logistic version of Equation 1

$$E(p_t) = \frac{\exp(S_t)}{1+\exp(S_t)} \qquad (2)$$

$$S_t = S_s + \delta_t + F_{sq} \qquad (3)$$

where p_t is the probability of survival of individual tree t. S_s determines the maximal survival probability of species s, δ_t determines the size-dependent reduction in survival probability of individual tree t, and F_{sq} determines the reduction in survival probability due to environmental selection. Additional niche processes such as biotic interactions can affect trait distributions (Cavender-Bares *et al.* 2004), and although I do not model them here, I believe that my my explicit models of niche limitations will increase my ability to disentangle different niche mechanisms.

Non-random spatial variation in a species' performance, as opposed to species spatial distributions, provides evidence for environmental selection that cannot be confounded or obscured with dispersal patterns (Uriarte *et al.* 2004). Limited dispersal can generate clumped distributions that are spuriously correlated to spatially autocorrelated environmental variation, which could in turn generate in spurious trait-environment correlations. Similarly, limited dispersal could generate spurious correlations between environment and environment-independent demographic rates. Spatial variation in a given species' performance provides stronger evidence for environmental selection. My strategy of comparing how a species' performance changes across environments is akin to conducting a series of observational common garden experiments, similar to those used to demonstrate intraspecific variation in genetic specialization to local environments (Nagy & Rice 1997).

In order to model variation in demographic rates due to environmental selection it is essential to account for the substantial portion of variation in demographic rates that is environment-independent (Uriarte *et al.* 2004). Growth and survival rates vary widely among species and can show dramatic ontogenetic changes (Davies 2001, Uriarte *et al.* 2004). Following Uriarte *et al.* (2004), species-specific growth and the effect (δ_i) of DBH on diametric growth rate is modeled using a log-normal function:

$$\delta_i = -\frac{1}{2}\left[\frac{\ln\left(\frac{DBH_i}{X_{0s}}\right)}{X_{bs}}\right]^2 \qquad (4)$$

where DBH_i is the DBH of individual i, X_{0s} is the DBH at which maximum growth or survival occurs for species s, and X_{bs} determines the dispersion of the function. The equation is the same for size-dependent survival, except that it is a function of the DBH of the largest stem for multiple-stemmed individuals. This log-normal function is well-supported for growth (Zeide 1993) and allows us to model U-shaped ontogenetic mortality (i.e. greatest mortality of seedlings and largest adults; Harcombe 1987), though it is flexible enough to model monotonic functions as well (e.g. when $X_{0s} \rightarrow 0$). I constrain species-specific ontogenetic parameters to hyper-distributions:

$$X_{0s} \sim \gamma\left(k_0, \theta_0\right) \qquad (5)$$

$$X_{bs} \sim \gamma\left(k_b, \theta_b\right) \qquad (6).$$

Gamma distributions are appropriate because they constrain parameters to be positive and they can model the strong right skews seen in distributions of individual species

parameters found by Uriarte *et al.* (2004). Maximum radial growth for each species g_s is also modeled as a random variable

$$g_s \sim N\left(\mu_g, \sigma_{g^2}\right) \qquad (7).$$

Hyper-distributions of species-specific parameters are the same for growth and survival models.

I represent local environmental selection within a quadrat by making performance a Gaussian function of species traits and by allowing this function to vary in space. The Gaussian form follows assumptions of many studies that environmental selection reduces trait range and variance in a community (e.g. Kraft *et al.* 2008, Swenson & Enquist 2009). Additionally, if one assumes that traits describe niche variation along an environmental axis, then my form is similar to theoretical models of MacArthur & Levins (1967) and Tilman (2004) who assume Gaussian forms to species performance along a niche axis. In my model, each quadrat in the forest plot has a Gaussian filtering function describing the decay in performance as a species trait is farther from an optimum trait value. The filtering effect in quadrat q on species s with trait value T_s is

$$F_{sq} = -\frac{\left(T_s - \mu_q\right)^2}{2\sigma_q^2} \qquad (8)$$

where μ_q is the optimal quadrat trait value, or the trait value for which performance is not reduced and σ_q determines the strength of selection (as σ_q decreases selection becomes stronger). Note that the optimal trait value for a quadrat need not occur within the range of trait values of the species present, so that in some quadrats all species could have

performance reduced below their respective maxima. This allows us to model environmental gradients where all species perform best in good conditions, but in poor quality locations species with certain functional traits have the least reduction in performance (e.g. Sterck *et al.* 2011).

I assume that selection is determined by environmental conditions (Weiher *et al.* 1998, Cornwell & Ackerly 2009). I model the optimal trait value as a function of the environment. The optimal trait value in a quadrat is linearly related to a vector of measured local environmental conditions $\boldsymbol{X_q}$

$$\mu_q = \mu + X_q \beta + \epsilon_q \qquad (9)$$

where μ is the mean plot-wide trait optimum, $\boldsymbol{\beta}$ is a vector of environmental effects on trait optima, and ε_q is the random error in the optimum. The filtering function varies among quadrats q and affects all species in a quadrat. Random errors in quadrat specific filtering parameters are constrained to hyper-distributions:

$$\epsilon_q \sim N\left(0, \sigma_{\mu^2}\right) \qquad (10)$$

where σ_μ is the standard deviation of optimal quadrat trait values, and

$$\sigma_q \sim Inv-\gamma\left(k_F, \theta_F\right) \qquad (11).$$

I included error terms at the level of the individual (often comprised of multiple stems) and the quadrat. The observed growth of individual stem i of species s (y_i) is the expected growth plus random error

$$y_i = \exp\left(g_s + \delta_i + F_{sq} + \upsilon_q + \tau_t\right) + \varepsilon_i \qquad (12)$$

where ε_i is individual stem error, τ_t is tree-level error (accounting for covariance among multiple stems of the same tree), and υ_q is error at the quadrat level. Error distributions are Gaussian with mean 0.

The full joint conditional posterior probability is included in the Appendix. Parameters were given diffuse proper priors and posterior distributions were estimated via Markov Chain Monte Carlo (MCMC) with a Gibbs sampler. I used JAGS 3.0 to implement sampling (http://mcmc-jags.sourceforge.net/). Most chains converged within 10 k samples, although a few were slower at converging and required up to 200 k samples. Initial samples prior to convergence were discarded (MCMC chain "burn-in") when reporting posteriors.

Comparisons of selection along environmental and trait axes

I studied a model of growth and a model of survival for each trait-environment combination described below. I estimated model parameters for separate models for each trait and the first two principal components of traits. I modeled the performance of all species with data along a given trait axis. I fit each trait model with four quadrat-level environmental variables (Eqn. 9) potentially important to community variation and relatively uncorrelated to each other: topographic convexity (Webb & Peart 2000), topographic slope, available nitrogen and available phosphorous. I limited the number of environmental variables in the model to avoid problems with identifiability of collinear covariate effects (Table A.1).

I compared spatial variation in selection and the strength of selection across

different trait axes. I assessed spatial variation in selection in two ways: (1) the standard deviation of quadrat optimal trait values (μ_q) and (2) the average species variance in selection effects experienced across the plot, weighted by species abundance. The first metric describes how the best trait value for local environments varies in space. However, the optimal trait values do not indicate the strength of selection and the impact of selection across species. The second metric accounts for the strength of selection and its effects on all species in the community. The strength of filtering along a trait axis (irrespective of spatial variation in selection) was measured with (1) the average of quadrat-specific strength of selection parameters, σ_q and (2) the median estimated loss in growth or probability of survival due to selection across all stems.

I compared models of growth versus survival for the same trait in order to study life-history trade-offs and their variation in space. Environmental conditions that cause spatial variation in performance may affect species growth and mortality in correlated ways if good conditions promote both growth and survival. Under this hypothesis, optimal quadrat trait values for growth should be positively correlated to optimal trait values for survival. Alternatively, environmental conditions may affect different aspects of demography, so that conditions favoring certain species for growth in one location may increase the mortality of those same species. The spatial relationship between selection for growth versus survival has implications for natural selection on life-history, in the latter case heterogeneity could generate life history trade-offs.

Comparison analyses

I compared results from my model to those from three additional techniques that may provide evidence for environmental selection. These analyses tested whether environmental selection axes that I estimated were concordant with 1) the mean trait values of species in a quadrat, 2) the difference in neighborhood trait diversity between trees that survived versus died (Uriarte *et al.* 2010), or 3) the change in trait diversity in quadrats from one census to the next. Analyses are explained in detail in the Appendix.

RESULTS

Growth models

I determined which environmental-trait axes showed the strongest selection and the most spatial variation in selection. Fitted selection functions differed widely, with some showing little spatial variation and very strong effects, and others showing large spatial variation with weaker selection. When referring to point estimates of parameters below I use the mean of MCMC posterior samples. Across traits, the expected strength of selection, which is the average precision parameter of Gaussian selection functions $1/\sigma_q^2$, was significantly negatively correlated to variance in quadrat trait optima (Spearman's rank correlation, $\rho = -0.82$, $p = 0.03$; Figure 4.2). The strongest environmental selection on growth, as determined by the lowest σ_q, occurred along an axis of species maximum height variation and PC2 (negatively correlated to maximum height; $r = -0.6$) had the next lowest σ_q (Table 4.2). As quadrat convexity and soil available N increased, species with smaller maximum height were favored for growth (Figure 4.3). The most variable

(but weaker) filtering, as measured by variance in quadrat trait optima μ_q, occurred along an axis of wood density, where quadrats with greater convexity and greater available N favored species with greater wood density. Convexity and available N were the environmental variables most important across multiple axes of trait-based selection, being correlated to optimal SLA, height, leaf succulence, and PC1 (i.e. 95% CI for β excluded zero).

Among traits, maximum height variation was associated with the greatest median proportion of growth lost due to fitted selection functions. However, for traits such as wood density with weaker selection there were major selection effects because fitted quadrat trait optima were far from the trait values of most species. Estimated wood density selection functions for many quadrats were monotonic because optimal wood density values were greater than maximum wood density across species (Table 4.2). The optimal trait values of PC1 varied widely and based on variance in species-specific performance across the plot, selection along PC1 was most heterogeneous.

Survival models

As with growth, the expected strength of selection on a given trait (average of $1/\sigma_q^2$) was negatively correlated to variance in quadrat optima of that trait (Spearman's rank correlation, $\rho = -0.82$, $p = 0.03$). The strongest environmental selection on survival, as determined by the lowest σ_q, occurred along PC1. Wood density (negatively correlated to PC1, $r = -0.32$) had the next lowest σ_q (Table 4.2, Figure 4.4). As quadrat slope became steeper and soil available P increased, species with greater PC1 scores were favored for

survival. The most spatially variable (but weaker) selection, as measured by variance in quadrat trait optima μ_q, occurred along an axis of leaf area. Quadrats with steeper slope and greater available N favored species with larger leaves. Available P was the environmental variable associated with selection for survival along the most trait axes (i.e. the most trait models where 95% CI for $\beta_{Ava.\ P}$ excluded zero). Local optima for leaf succulence, maximum height, wood density, and PC1, were correlated to available P (Table 4.2, Figure 4.5).

Among traits, the greatest median proportion of probability of survival was lost due to selection along an axis of wood density. Wood density had the greatest spatial heterogeneity in selection based on variance in species-specific survival due to selection across the plot.

Evidence for demographic trade-offs along environmental gradients

Optima for growth vs. survival were significantly (α=0.05) positively correlated for four traits (leaf area, leaf succulence, maximum height, and PC2) and leaf area showed the strongest correlation (Spearman's rank test, $\rho = 0.25$, $p < 10^{-10}$). While these optima were correlated, correlations were very noisy and the slope of the relationship was not 1:1. Quadrat and plot-wide trait optima had large differences between growth and survival for the same traits, indicating demographic trade-offs along trait axes (Table 4.2). When trait optima were correlated to environmental variables (i.e. 95% CI of β excluded zero) for one demographic variable such as growth, trait optima for the other demographic variable, survival, were correlated to the environment in the same direction, or were

uncorrelated (Table 4.2).

Comparison to additional techniques

Comparison statistical analyses using static data were concordant with my results in some cases (Appendix). Analyses using dynamic demographic data were more closely related to my results.

DISCUSSION

Using a novel approach, I quantified multiple trait axes of environmental selection in a diverse tree community. Selection along an axis of maximum height variation was the strongest for growth limitation and optimal maximum height was negatively correlated to quadrat convexity and available N. Greater quadrat convexity may be associated with increased exposure to wind and with reduced soil moisture (Daws *et al.* 2002), both of which could favor species with shorter growth forms. Greater convexity and steeper slope have been associated with an increased rate of gap-formation in Malaysia, higher light availability, and potentially a greater risk of mortality for large trees (Ohkubo *et al.* 2007). Community trait diversity can differ based on disturbance regime. Ding *et al.* (2011) found that lowland shifting cultivation forests had significantly less trait clustering and thus weaker trait-associated selection than old growth forests in Hainan.

I found quadrats with greater available P favored species with greater SLA for survival and growth, although quadrats with higher available N favored growth of

species with lower SLA. Taiwanese subtropical forests are thought to be highly P-limited (Wu *et al.* 2007). Across Amazonia species occupying higher fertility soils tend to have higher SLA (Fyllas *et al.* 2009). More acquisitive species typically have high SLA (relative to conservative species) that allows greater carbon fixation when light and water are abundant (Sterck *et al.* 2006, Sterck *et al.* 2011). In my study, greater SLA was favored for growth in more concave quadrats, which should have greater soil moisture. However convex quadrats tend to have greater light availability at Fushan due to typhoon disturbance on ridges. This discrepancy may signify that reduced soil moisture on ridges has greater SLA-mediated selection effects than does increased light availability on ridges.

Survival selection along an axis of wood density was strongest and most spatially variable among traits. Slope was the strongest correlate of wood density survival selection, favoring lighter wood on steeper quadrats and heavier wood species on more level quadrats. Like convex locations, steep slopes are often associated with greater levels of disturbance (Ohkubo *et al.* 2007), shorter canopy height, and greater light availability. High light availability may increase the survival of species with light wood that have low survival in shade (Augspurger 1984). Greater available P also favored survival of species with heavier wood. My result is consistent with findings that tropical species with greater wood density tend to occupy poorer soils at the landscape scale (Gourlet-Fleury *et al.* 2011). However, increased available N favored growth of high density wood species. The fact that wood density selection had the greatest spatial variation may signify that it is an important axis of spatial niche differentiation.

For four trait axes, SLA, leaf succulence, wood density and PC1, nearly all species grew best toward one extreme of the environmental gradient (concave quadrats and quadrats with low available N), and away from this extreme there was selection on growth based on traits. This pattern fits the variation in performance along light and water gradients in Bolivian dry forest observed by Sterck *et al.* (2011), where all species performed best in high light and high water availability, but traits predicted decreases in performance under low light and dry conditions.

Environmental gradients associated with trait selection were often different between growth and survival, which could be a consequence of 1) distinct ecophysiological pathways affecting growth and survival and 2) demographic trade-offs where increased growth in one environment is associated with increased mortality in another environment. Additionally, environmental demographic trade-offs may take different forms addressed by different models (Russo *et al.* 2008).

The effects of small-scale variation in selection on spatial variation in community composition are limited by the species pool in the plot, so that selection effects are partly determined by forces governing species pools. Species pools are shaped by forces acting across larger spatiotemporal scales than a 25-ha plot. The frequency and spatial configuration of environmental conditions across larger scales will likely shape the species pool via evolution, speciation, extinction, and long-distance migration. Part of the variation in strength of selection among traits may be due to environmental selection along these trait axes across a larger region. Fushan FDP is found on the lower slopes of the steep mountain range of central Taiwan. Similar climatic conditions to Fushan are

distributed roughly in a belt around the island. Taiwan formed ~9 mya and has been connected to mainland Asia via land bridges during glacial periods (and as recently as ~13 kya; Voris 2000). Accordingly, Taiwanese flora are primarily Asian in origin and approximately 25% of Taiwanese vascular plant species are endemic (Chiang & Schaal 2006). Integrated analysis of dynamics from a larger network of plots could reveal selection across larger spatiotemporal scales. Researchers are beginning to use trait-based functions to model large scale species distributions (Pollock *et al.* 2011, Reif & Flousek 2012).

Environmental selection has been proposed as an important mechanism of community assembly on forest plots, but it has rarely been documented where dispersal effects were conclusively separated from environmental effects. By studying individual trees through time I have avoided this problem. Typically the existence of environmental selection is inferred from species-trait distributions (e.g. Kraft *et al.* 2008, Swenson & Enquist 2009). My approach is related to that of Clark *et al.* (2010) who tracked spatial variation in tree dynamics in the Southeast USA. The authors found that different species occurring in the same neighborhood tended to have asynchronous dynamics, even though across large areas species average dynamics were synchronous, suggesting that small-scale selection may cause locally asynchronous dynamics. Few studies have explicitly linked dynamics to species traits and environmental selection to measured environmental gradients as I have (but see Cornwell & Ackerly 2009).

I found that my estimated selection functions were not highly concordant with static distributions, suggesting the role of additional processes in affecting tree

distributions on the plot (e.g. dispersal, Appendix). The effects of environmental selection on spatial distributions are partly dependent on the spatial scale of analysis and the level of autocorrelation present in the environment (Pinto & MacDougall 2010). My finding that trait-environment distributional correlations were incongruent with environmental performance filters is unsurprising given that dispersal can obscure environmental effects on distribution. Sink populations within suboptimal habitat of a forest plot can be maintained by continued dispersal (Zuidema et al 2010). Similarly, Pinto & MacDougall (2010) found that distribution shows weaker environmental patterns than performance measures, probably due to dispersal patterns. However, static distributional patterns are affected by demographic variation across the life-cycle, including fecundity and recruitment, whereas my study focused on growth and survival of trees over 1 cm DBH.

Future directions

My model is a flexible framework that allows for the addition of more life history stages and the inclusion of additional community assembly processes. Future research that integrates filtering effects on fecundity could help us complete the modeled life-cycle to make stronger conclusions about the importance of filters for maintenance of diversity (Clark *et al.* 2010, Uriarte *et al. In press*). Once the full life cycle is included, the model can be used to make stochastic projections about future community trajectories in changing environments. Additionally, future efforts could incorporate biophysical models that predict inter-specific variation resource acquisition and demography as a function of

the environment and functional traits (Sterck *et al.* 2006, Sterck *et al.* 2011). I used my model to estimate multiple axes of niche-based selection for nearly every species in a tree community. Selection functions and surfaces (e.g. Figure 4.5) could be used in other studies such as those that study community trait evolution (Hubbell 2006). Note that my environmental selection functions are similar to environmental fitness functions in evolutionary biology, and it is likely that advances can be made through shared approaches between the fields (Vellend 2010).

Future studies could estimate a more realistic surface of environmental selection, whereas here I have conveniently estimated it at the level of square quadrats. Additionally, different functional forms of selection (e.g. multi-modal) and explicit links between environmental conditions and strength of selection (Russo *et al.* 2008) could be incorporated. Experimental manipulations of environmental conditions in forest plots could test the environmental selection axes that I inferred.

Conclusions

I found that environmental-based trait selection varied in strength across different axes of environmental, functional trait, and demographic variation. These patterns were not always the same as those observed in static data. Functional community dynamic models offer a promising method of studying the factors driving spatiotemporal variation in tree communities.

Tables

Table 4.1. Cross-trait correlations (Pearson product-moment correlation coefficient). The first two principal component axes of the traits are also shown. Note that wood density was not included in the calculation of principle components because there were substantially fewer species with wood density data than there were for other traits.

	SLA	Leaf succulence	Max. height	Wood density	PC1	PC2
Leaf area	0.21	-0.01	0.11	-0.40	0.22	-0.83
SLA		-0.36	-0.41	-0.39	0.89	-0.06
Leaf succulence			0.02	-0.15	-0.59	0.22
Max. height				0.30	-0.62	-0.60
Wood density					-0.32	0.12
PC1						0.00

Table 4.2. Posterior parameter estimates. For the effects of environmental variables (β), 95% Credibility Intervals are shown, those in bold are those that exclude zero. μ is the mean of the hyper-distribution of quadrat trait optima (μ_q) and it is shown +- the standard deviation of quadrat optima [s.d.(μ_q)]. E(σ_q) is the mean of the inverse-gamma hyperdistribution of all σ_q and gives the strength of filtering. Estimates of μ_q, σ_μ, and σ_q, are taken from posterior medians.

	Trait	Convexity Effect (β_C)	Ava. N Effect (β_N)	Ava. P Effect (β_P)	Slope Effect (β_S)	Optimal trait value μ+-s.d.(μ_q)	Inverse strength of selection, E(σ_q)
Growth models	Leaf area	-0.07, 0.19	-0.17, 0.13	-0.30, 0.01	**0.02, 0.40**	0.69 +- 0.22	2.69
	SLA	**-3.53, -0.67**	**-1.99, -0.15**	-0.06, 2.26	-2.06, 0.10	-1.51 +- 2.00	8.09
	Leaf succulence	**0.02, 1.25**	**0.04, 1.14**	-0.72, 0.19	-0.28, 0.85	1.00 +- 0.83	6.13
	Maximum height	**-1.45, -0.13**	**-1.02, -0.06**	-0.20, 0.32	-0.25, 0.15	0.13 +- 0.57	2.45
	Wood density	**2.61, 16.83**	**0.85, 12.47**	-7.04, 1.46	-1.95, 6.42	7.44 +- 7.66	41.84
	PC1	-1.93, -0.59	**-1.35, -0.24**	-0.09, 1.41	-1.22, 0.15	-1.10 +- 2.26	6.97
	PC2	-0.08, 0.42	-0.29, 0.09	-0.29, 0.16	-0.09, 0.32	-0.59 +- 0.24	2.61
Survival models	Leaf area	-0.15, 0.05	**0.02, 0.23**	-0.13, 0.07	**0.08, 0.33**	-0.24 +- 0.51	1.8
	SLA	**-0.06, -0.00**	-0.03, 0.03	**0.04, 0.10**	**0.04, 0.10**	-0.65 +- 0.13	1.4
	Leaf succulence	-0.04, 0.06	**0.01, 0.13**	**-0.20, -0.05**	-0.07, 0.04	-0.06 +- 0.25	1.41
	Maximum height	-0.10, 0.03	-0.07, 0.06	**-0.22, -0.06**	**-0.24, -0.07**	0.72 +- 0.48	1.5
	Wood density	**0.00, 0.11**	-0.10, 0.01	**-0.16, -0.03**	**-0.25, -0.11**	0.61 +- 0.28	1.35
	PC1	-0.04, 0.03	-0.04, 0.04	**0.04, 0.13**	**0.00, 0.11**	-0.31 +- 0.13	1.28
	PC2	-0.04, 0.13	-0.15, 0.02	-0.00, 0.17	-0.03, 0.15	-0.50 +- 0.44	1.57

Figures

Figure 4.1. Illustration of environmental selection filtering of tree performance across quadrats of a forest plot. Hypothetical tree locations are indicated by white circles. In each quadrat *q*, a different Gaussian selection function is estimated with a local optimal trait value (μ_q, the mean of the Gaussian) and a local strength of selection (determined by σ_q, the standard deviation of the Gaussian). Small σ_q indicates rapid decline in performance for a small change in trait value, while large σ_q indicates weak selection. Each quadrat has separately estimated Gaussian parameters, constrained by hyper-distributions. Note that species-specific ontogenetic growth patterns are also a part of the models.

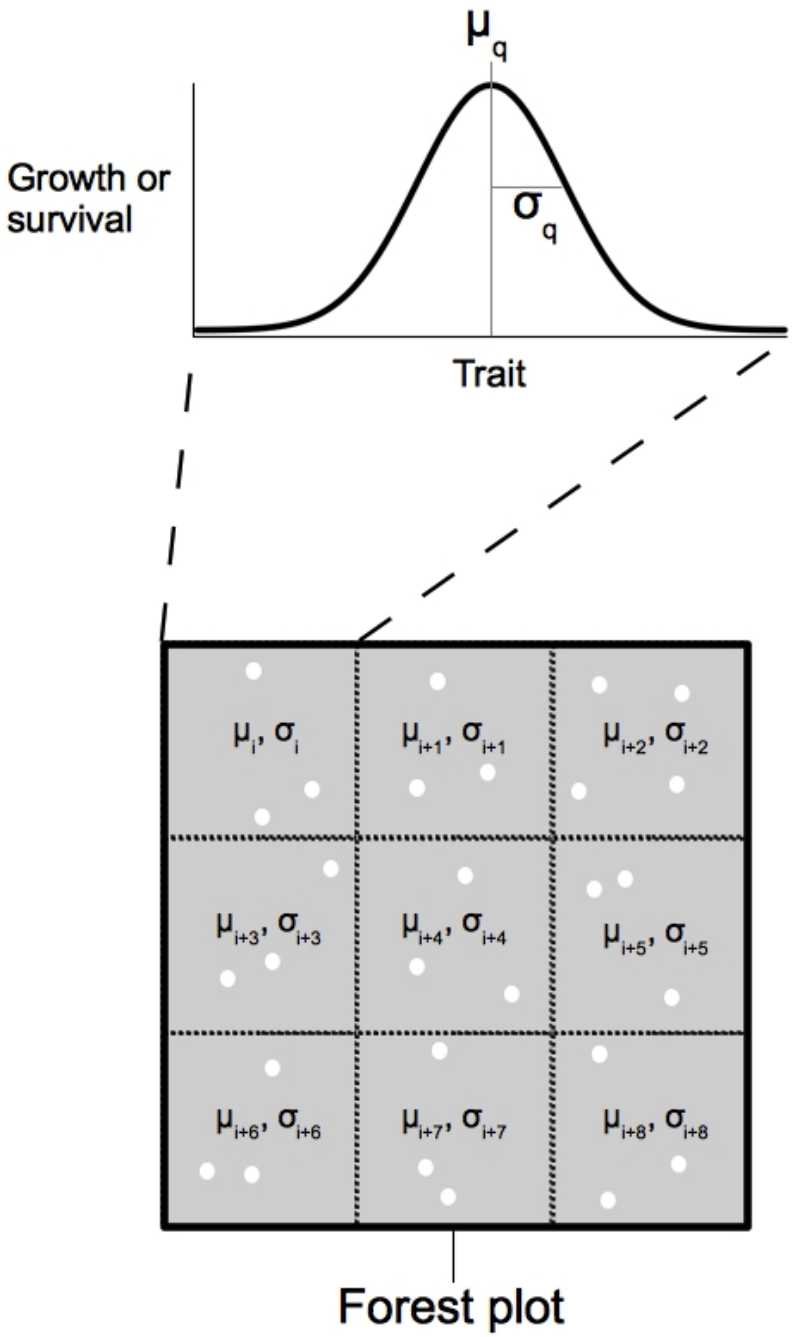

μq
σq
Growth or survival
Trait
μi, σi
μi+1, σi+1
μi+2, σi+2
μi+3, σi+3
μi+4, σi+4
μi+5, σi+5
μi+6, σi+6
μi+7, σi+7
μi+8, σi+8
Forest plot

Figure 4.2. The average strength of selection on a given trait axis ($1 / \sigma_q^2$) declines as the spatial variation in optimal trait values (μ_q) increases.

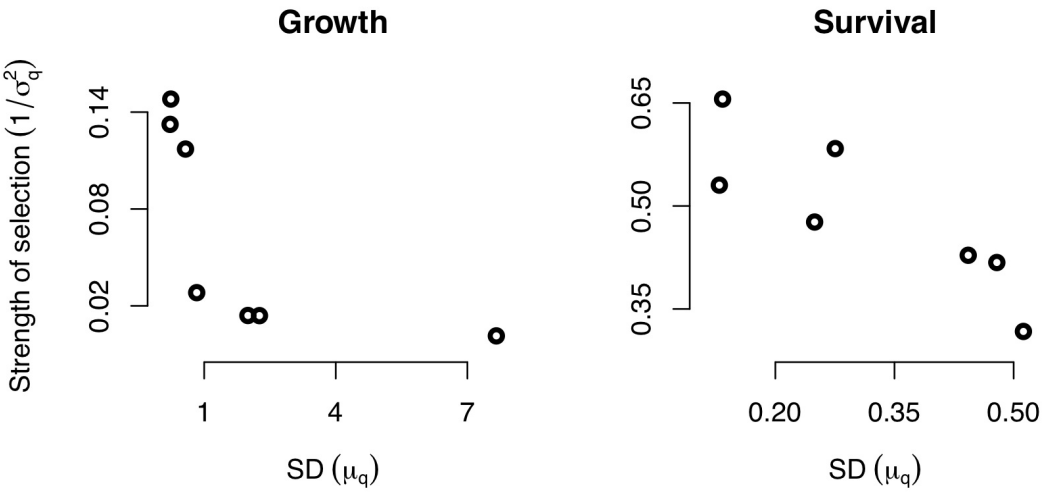
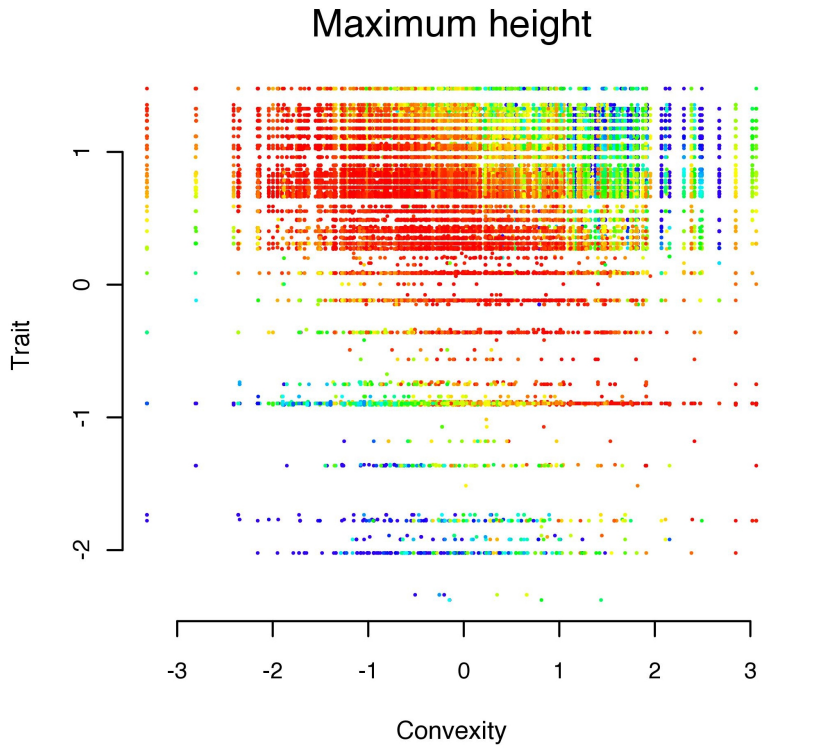


Figure 4.3. Proportional growth of individual trees due to selection on maximum height. Species with the optimal value of maximum height for their quadrat, μ_q, have proportional growth equal to unity (red dots). Species selected against because of their trait value are shown in blue, meaning their proportional growth was <0.75 the expected in the absence of filtering. As quadrat convexity increases, there is a decrease in the trait value of maximum height that is optimal for growth. Species wood density (y-axis) and quadrat slope (x-axis) are standardized to have mean zero and unit variance.


Maximum height
Trait
1
0
-1
-2
-3
-2
-1
0
1
2
3
Convexity

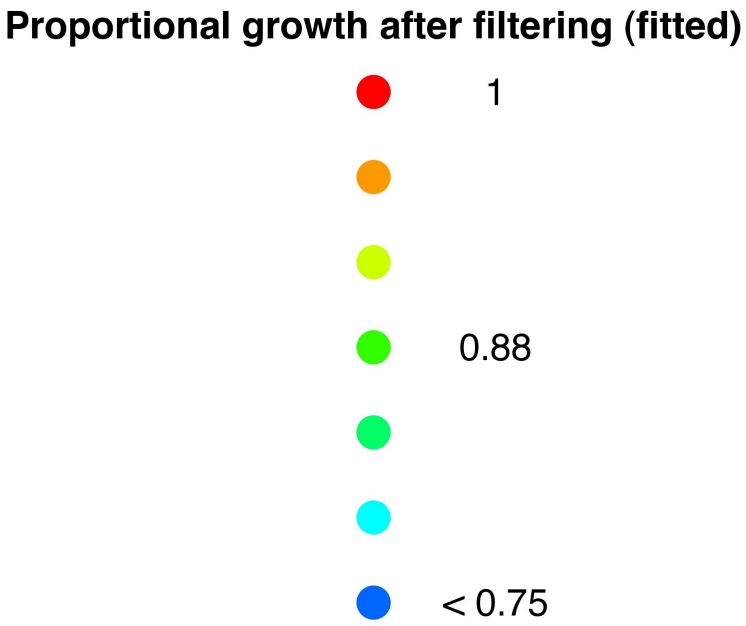
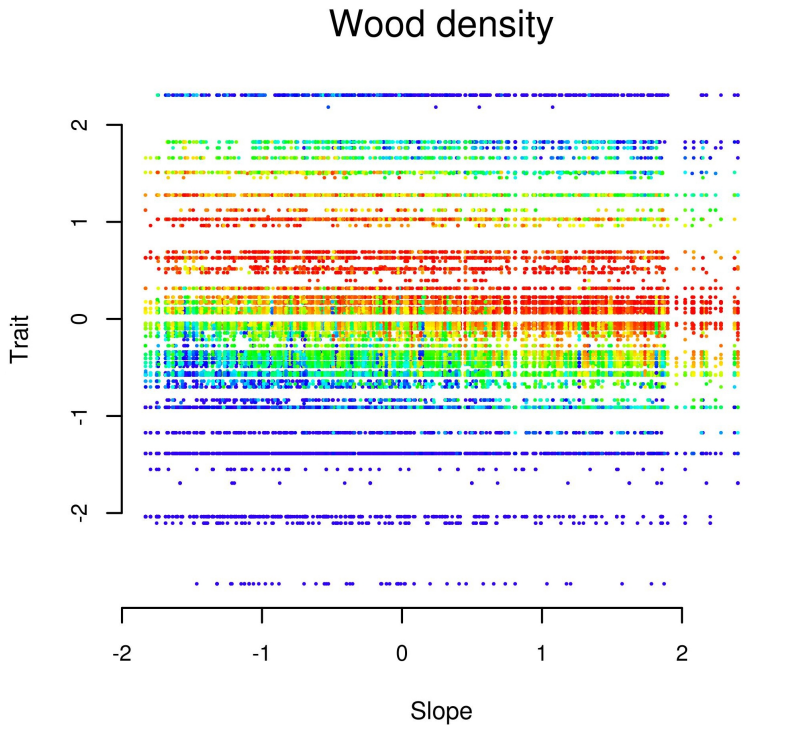

Proportional growth after filtering (fitted)
1
0.88
< 0.75

Figure 4.4. Proportional survival probability of individual trees due to selection on wood density. Species with the optimal value of wood density for their quadrat, μ_q, have proportional survival equal to unity (red dots). Species selected against because of their trait value are shown in blue, meaning their proportional survival was <0.5 the expected in the absence of filtering. As quadrat slope increases, there is a decrease in the trait value of wood density that is optimal for growth. Species wood density (y-axis) and quadrat slope (x-axis) are standardized to have mean zero and unit variance.


Wood density
Trait
2
1
0
-1
-2
-2
-1
0
1
2
Slope

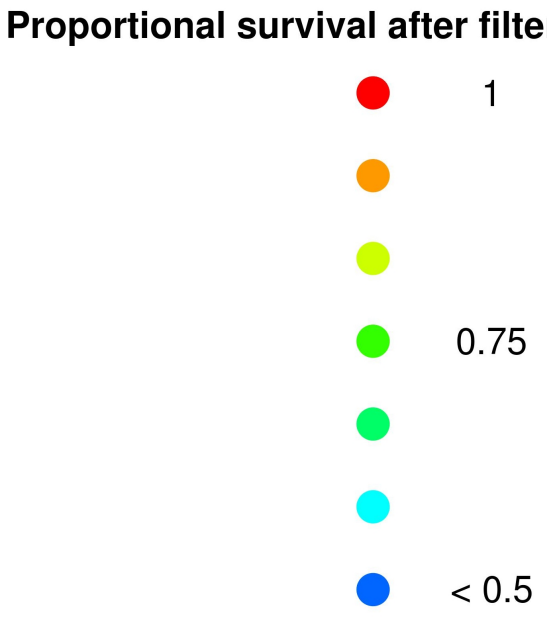
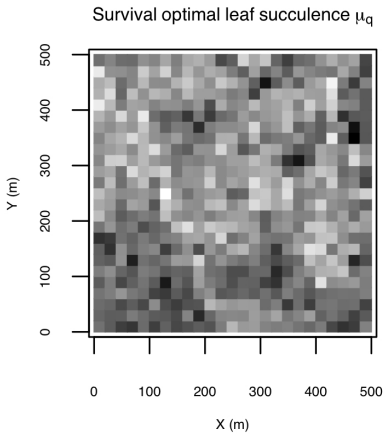
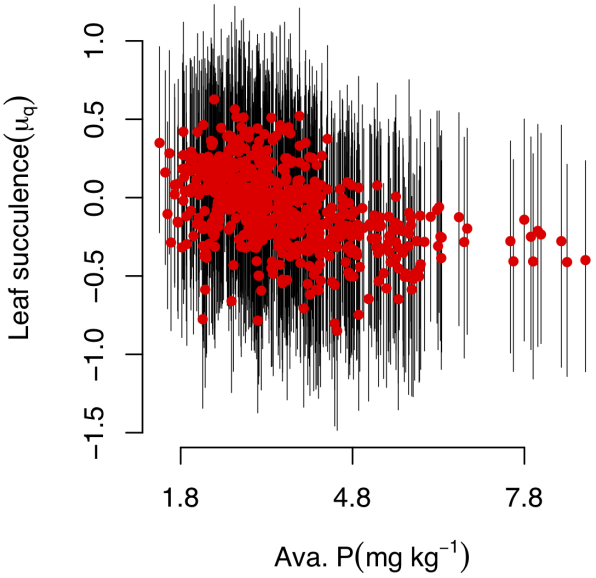
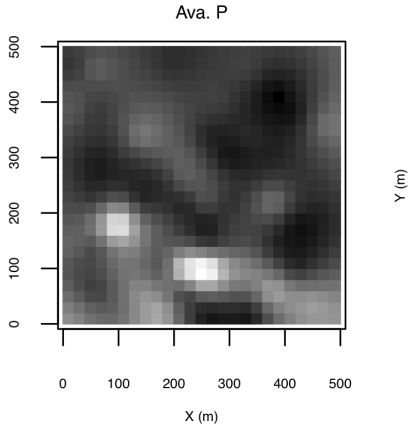

Proportional survival after filtering (fitted)
1
0.75
< 0.5

Figure 4.5. As quadrat available P increases, the optimal value of leaf succulence decreases (upper right). Red dots show posterior means of optimal quadrat values of leaf succulence μ_q, black lines indicate 95% CIs. A map of posterior means of optimal leaf succulence μ_q for all quadrats is shown, with white indicating more succulent leaves (upper left). Leaf succulence values are standardized to have mean zero and unit variance. A map of available P at the quadrat level is shown, with white indicating high available P.


Survival optimal leaf succulence μ_q
Y (m)
0
100
200
300
400
500
X (m)


Leaf succulence(μ_q)
1.0
0.5
0.0
−0.5
−1.0
−1.5
1.8
4.8
7.8
Ava. P(mg kg^{-1})


Ava. P
Y (m)
0
100
200
300
400
500
X (m)

Appendix

Additional information on Chapter IV

Joint posterior probability

The probability of the model parameters given the data is proportional to the likelihood of the data multiplied by the prior probability of the parameters. Stated formally

$$
\begin{aligned}
&p\left(g_s, X_{0s}, X_{bs}, \beta, \mu, \sigma_q, \epsilon_q, \upsilon_q, \tau_t \sigma_\epsilon \middle| y_i, DBH_i, T_s\right) \propto \\
&\prod_{i=1}^{I} Normal\left(y_i \middle| g_s, X_{0s}, X_{bs}, \beta, \mu, \sigma_q, \epsilon_q, \upsilon_q, \tau_t, DBH_i, T_s\right) \\
&\times \prod_{s=1}^{S} Normal\left(g_s \middle| \mu_g, \sigma_g\right) \\
&\times \prod_{s=1}^{S} Gamma\left(X_{0s} \middle| k_{0,}, \theta_0\right) \\
&\times \prod_{s=1}^{S} Gamma\left(X_{bs} \middle| k_b, \theta_b\right) \\
&\times \prod_{q=1}^{Q} Inv-Gamma\left(\sigma_q \middle| \alpha_\sigma, \beta_\sigma\right) \\
&\times \prod_{q=1}^{Q} Normal\left(\epsilon_q \middle| 0, \sigma_\mu\right) \\
&\times \prod_{q=1}^{Q} Normal\left(\upsilon_q \middle| 0, \sigma_\upsilon\right) \\
&\times \prod_{t=1}^{T} Normal\left(\tau_t \middle| 0, \sigma_\tau\right) \\
&\times Normal\left(\beta \middle| 0, 10^2\right) \\
&\times Normal\left(\mu \middle| 0, 10^2\right) \\
&\times Normal\left(\mu_g \middle| 0, 10^2\right) \\
&\times Gamma\left(k_0 \middle| 10^{-3}, 10^3\right) \\
&\times Gamma\left(\theta_0 \middle| 10^{-3}, 10^3\right) \\
&\times Gamma\left(k_b \middle| 10^{-3}, 10^3\right) \\
&\times Gamma\left(\theta_b \middle| 10^{-3}, 10^3\right) \\
&\times Gamma\left(\alpha_\sigma \middle| 10^{-3}, 10^3\right) \\
&\times Gamma\left(\beta_\sigma \middle| 10^{-3}, 10^3\right) \\
&\times Gamma\left(\sigma_\mu \middle| 10^{-3}, 10^3\right) \\
&\times Gamma\left(\sigma_\upsilon \middle| 10^{-3}, 10^3\right) \\
&\times Gamma\left(\sigma_\tau \middle| 10^{-3}, 10^3\right) \\
&\times Gamma\left(\sigma_\epsilon \middle| 10^{-3}, 10^3\right)
\end{aligned}
$$

where parameters are defined in the main text. All priors are uninformative.

Comparison statistical analyses

I compared results from my model to those from three additional techniques that may provide evidence for environmental selection. The first method used static tree distributions. I determined correlations between the environmental variables in quadrats and the mean species traits of stems in the quadrat, weighted by the abundance of each species. Selection effects may change over time, such that patterns change across size classes (Poorter 2007, Swenson & Enquist 2009). I stratified this analysis by tree size class and determined if environment-trait correlations changed across size classes.

I compared results from my survival models to analyses of the effects of neighborhood trait similarity on tree survival. Environmental selection is expected increase the similarity of co-occurring, surviving trees, while local niche differentiation within environments is expected to cause greater mortality among co-occurring trees with similar traits (Uriarte *et al.* 2010). I calculated the abundance-weighted mean trait distance (MTD) between trees within 20 m neighborhoods of each focal tree (Webb 2000, Webb *et al.* 2002, Uriarte *et al.* 2010). I compared the mean MTD for surviving trees to the mean MTD of trees that died between censuses. I only considered trees alive in the first census. Following Uriarte *et al.* (2010), I then tested whether trees that survived had significantly different MTD from those that died, while accounting for interspecific differences in mean MTD. I constructed a general linear mixed model where MTD was the response, tree survival was a fixed effect and species was a random effect. However, my test differed from Uriarte *et al.* (2010) because I also considered rare species.

I compared my results to four additional metrics that may provide evidence of environmental selection. Selection may reduce trait diversity, range, and variance. I compared the trait diversity (Petchey & Gaston 2002), range, variance, and abundance-weighted variance of species traits in each quadrat in the 2003 census to trait metrics of individuals that survived until 2008. For metrics calculated with species presence-absence in quadrats (i.e. trait diversity, range, and variance), the change in each statistic was compared to null model simulations of extinction in quadrats. In simulated extinctions a quadrat lost the same number of species from 2003 to 2008 as observed, and the probability of a species going extinct from a quadrat was proportional to its abundance in the quadrat. For abundance weighted trait variance, the null simulation model was that each quadrat lost a given number of individuals (equal to the observed number dead) but that each individual in the quadrat had an equal probability of dying. I ran 1000 Monte Carlo simulations of death and species loss for each quadrat.

Results for comparison to additional techniques

Mean species trait values averaged among stems in quadrats were significantly correlated to many environmental variables (Table A.2). Some of these static trait-environment correlations were consistent with findings from demographic selection models. For example, quadrat optimal SLA was negatively correlated to convexity (95% CIs of β; -3.54, -0.67 for growth; -0.06, -0.00 for survival) and quadrat mean SLA was also decreased with greater convexity (ANOVA, slope of convexity effect = -0.06, $p<10^{-6}$). my model found that species of greater maximum height were favored for growth in

concave quadrats but mean abundance weighted species maximum height was positively correlated to quadrat convexity (ANOVA, slope of convexity effect = 0.03, p = 0.002). However, when stratifying this static pattern into DBH classes, the positive relationship between convexity and maximum height existed only for the smallest DBH classes, and then becomes non-significantly negative at larger DBH-classes. This pattern is consistent with selection against species of high maximum height in convex quadrats acting over time. In some cases, changes in quadrat mean traits across DBH classes were inconsistent with my estimates of selection (Table A.3).

Comparisons between the trait neighborhoods of live versus dead trees were partially consistent with my selection model results. The trait diversity in neighborhoods of surviving trees was significantly less than that of dying trees as measured along maximum height and PC2 axes, and these were also the two traits with the strongest selection parameters (σ_q) for growth (linear mixed effects model, $p < 10^{-5}$ for each). However, diversity of all other traits was greater in neighborhoods surrounding live trees than those surrounding dead trees (linear mixed effects model, $p < 0.01$ for each).

The change in quadrat trait diversity metrics from trees in 2003 to survivors in 2008 partially supported results from my selection models. The observed loss in quadrat trait diversity was greatest relative to the null simulations along an axis of species maximum height (Figure A.1) and three out of the four trait metrics showed significant loss of maximum height diversity (empirical p-values from Monte Carlo simulations, $\alpha=0.05$). Maximum height was also the trait with the strongest growth selection parameters and with the greatest median reduction in growth due to fitted selection

functions. When focusing on trait variance weighted by abundance, which is similar to my selection models in that it accounts for abundance, 5 out of 7 traits showed significantly greater loss in trait variance due to death than null simulations, consistent with an important role for selection. The other two traits showed significantly less loss in trait variance than expected from simulations (Figure A.1).

Tables

Table A.1. Correlation between four variables used in models (convexity, OC, available N, available P), and the first four principal components axes used in a separate set of models.

	Convex.	**OC**	**Ava. N**	**Ava. P**	Elevatior	Slope	pH water	pH KCl	Conduct.	AvaK	Ca	Mg	K	Na
Convex.		0.073	0.064	0.009										
OC			0.533	0.488										
Ava. N				0.088										
PC1	-0.010	0.359	0.285	0.180	-0.038	-0.116	-0.021	0.020	0.309	0.438	0.304	0.423	0.427	-0.016
PC2	0.355	0.245	0.168	0.118	0.475	0.268	-0.150	-0.514	0.044	-0.033	-0.220	-0.011	-0.046	0.365

Table A.2. Mean stem trait value correlations to quadrat environments (ANOVA). Fixed-effect slopes of environmental variables are shown.

Trait	Convexity effect	p	Ava. N effect	p	Ava. P effec	p	Slope effec	p
Leaf area	-0.08	0.0000	-0.07	0.0000	0.02	0.0382	-0.01	0.1999
SLA	-0.06	0.0000	-0.01	0.3482	0.03	0.0336	-0.06	0.0000
Leaf succulenc	0.00	0.6887	-0.02	0.0169	0.02	0.0141	0.03	0.0024
Max. height	0.03	0.0025	0.00	0.5961	-0.04	0.0000	0.02	0.0354
Wood density	0.07	0.0000	0.04	0.0003	-0.02	0.0501	0.03	0.0019

Table A.3. Mean stem trait value correlations to quadrat environments (ANOVA), stratified by tree size class. Size classes were 1 = 1 cm ≥ DBH > 5 cm, 2 = 5 cm ≥ DBH > 10 cm, 3 = 10 cm ≥ DBH > 20 cm, and 4 = 20 cm ≥ DBH. Fixed-effect slopes of environmental variables are shown.

Trait	Environ. var.	Fixed effect	p	Size class
Leaf area	Convexity	-0.08	0.0000	1
		-0.11	0.0000	2
		-0.07	0.0001	3
		-0.03	0.0095	4
	Slope	-0.01	0.2711	1
		-0.02	0.3205	2
		-0.03	0.1076	3
		-0.04	0.0002	4
	Ava. N	-0.06	0.0000	1
		-0.09	0.0000	2
		-0.10	0.0000	3
		-0.02	0.1714	4
	Ava. P	0.02	0.0970	1
		0.03	0.1179	2
		0.06	0.0003	3
		0.03	0.0150	4
SLA	Convexity	-0.06	0.0001	1
		-0.02	0.0028	2
		-0.05	0.0000	3
		-0.03	0.0019	4
	Slope	-0.06	0.0002	1
		-0.05	0.0000	2
		-0.05	0.0000	3
		-0.03	0.0016	4
	Ava. N	-0.01	0.4159	1
		-0.01	0.1611	2

Table A.3 (continued).

Trait	Environ. var.	Fixed effect	p	Size class
Leaf succulence	Convexity	-0.01	0.5795	1
		-0.02	0.1293	2
		0.01	0.2566	3
		0.00	0.7172	4
	Slope	0.02	0.0222	1
		0.05	0.0001	2
		0.04	0.0013	3
		0.02	0.0619	4
	Ava. N	-0.02	0.0648	1
		-0.03	0.0115	2
		-0.04	0.0006	3
		0.00	0.6991	4
	Ava. P	0.02	0.0924	1
		0.06	0.0000	2
		0.00	0.7412	3
		0.00	0.9343	4
Maximum height	Convexity	0.03	0.0033	1
		0.00	0.8338	2
		0.00	0.8885	3
		0.00	0.6425	4
	Slope	0.02	0.0345	1
		-0.01	0.0630	2
		-0.01	0.0179	3
		-0.01	0.0227	4
	Ava. N	0.00	0.7223	1
		0.01	0.1933	2

Table A.3 (continued).

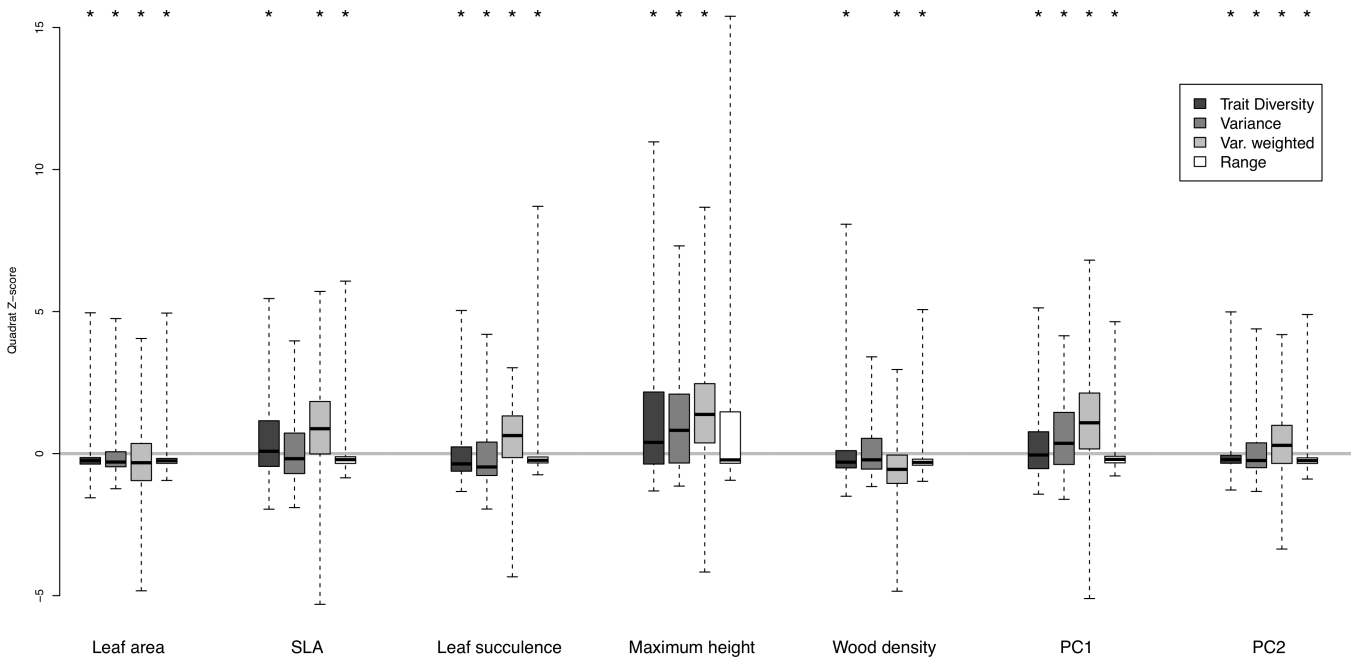
Trait	Environ. var.	Fixed effect	p	Size class
Wood density	Convexity	0.07	0.0000	1
		0.10	0.0000	2
		0.05	0.0000	3
		0.02	0.1126	4
	Slope	0.03	0.0016	1
		0.02	0.1011	2
		0.03	0.0168	3
		0.01	0.2559	4
	Ava. N	0.03	0.0012	1
		0.06	0.0000	2
		0.04	0.0002	3
		-0.01	0.4451	4
	Ava. P	-0.03	0.0101	1
		-0.01	0.5912	2
		0.00	0.7512	3
		0.03	0.0021	4
PC1	Convexity	-0.05	0.0004	1
		-0.02	0.0015	2
		-0.04	0.0000	3
		-0.02	0.0141	4
	Slope	-0.05	0.0007	1
		-0.05	0.0000	2
		-0.04	0.0000	3
		-0.03	0.0003	4
	Ava. N	-0.01	0.5378	1
		-0.01	0.1741	2

Table A.3 (continued).

Trait	Environ. var.	Fixed effect	p	Size class
PC2	Convexity	0.04	0.0000	1
		0.08	0.0000	2
		0.05	0.0000	3
		0.02	0.0063	4
	Slope	0.00	0.6000	1
		0.03	0.0071	2
		0.04	0.0017	3
		0.04	0.0000	4
	Ava. N	0.04	0.0000	1
		0.06	0.0000	2
		0.05	0.0000	3
		0.01	0.3448	4

Figures

Figure A.1. Four metrics designed to test evidence for environmental filtering based on trait diversity metrics. Each metric measures trait diversity of species in a quadrat. Weighted variance measures the variance of species traits of individuals in a plot. Z-scores for each quadrat are obtained by comparing observed quadrat loss in trait diversity due to mortality compared with null simulations of mortality. * indicates median is significantly different than 0 (Wilcoxon rank-sum test, $p < 0.05$).



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