

Effects of dispersal, shrubs, and density-dependent mortality on seed and seedling distributions in temperate forests

Janneke Hille Ris Lambers and James S. Clark

Abstract: Processes limiting recruitment of trees may have large impacts on forest dynamics. In this paper, we determined the effects of dispersal, shrubs (*Rhododendron maximum*), and density-dependent mortality on seed and seedling distributions of Southern Appalachian trees. We quantified the spatial distribution of seed rain, seed bank densities, first-year seedlings, and older than first-year seedlings in five vegetation plots. We fit models to these data assuming effects of limited dispersal, *R. maximum* (an understory shrub), and (or) density-dependent mortality (as well as a null model with none of these effects) and used best-fitting models to indicate which processes affected a particular species. We found that all factors examined limit species distributions, and thus, affect seedling dynamics. Seedling densities are higher near parent trees long after dispersal occurs. This pattern is less frequently observed for animal-dispersed species than for wind-dispersed species, presumably due to secondary dispersal of seeds by animals. Seedling densities of five species are decreased beneath *R. maximum*. Shade tolerance does not explain which species are affected, suggesting that factors other than low light are responsible for increased seedling mortality under this shrub. Our results suggest that density-dependent mortality affects four species, decreasing seedling densities close to parent trees. Dispersal, density-dependent mortality, and *R. maximum* all act in ways that may promote or limit diversity, illustrating that multiple factors are likely to control species diversity.

Résumé : Les processus qui limitent le recrutement des arbres peuvent avoir des impacts importants sur la dynamique forestière. Dans cette étude, nous avons déterminé les effets de la dispersion, des arbustes (*Rhododendron maximum*) et de la mortalité liée à la densité sur la distribution des graines et des semis d'arbres du sud des Appalaches. Nous avons quantifié la distribution spatiale de la pluie de graines, de la densité des banques de semis, des semis dans leur première année et de ceux de plus d'un an dans cinq placettes échantillons. Nous avons estimé les paramètres de modèles à l'aide de ces données en assumant les effets d'une dispersion limitée, du *R. maximum* (un arbuste du sous-étage) et (ou) de la mortalité liée à la densité (de même qu'un modèle de base ignorant tous ces effets) et nous avons utilisé les modèles avec le meilleur ajustement pour indiquer quels sont les processus affectant une espèce en particulier. Nous avons trouvé que tous les facteurs examinés limitent la distribution des espèces et par conséquent la composition de la communauté. La densité des semis est plus élevée à proximité des arbres parents longtemps après qu'il y ait eu dispersion. Ce patron est observé moins fréquemment pour les espèces zoochores que pour les espèces anémochores, probablement dû fait d'une dispersion secondaire des graines par les animaux. La densité des semis de cinq espèces diminue sous *R. maximum*. La tolérance à l'ombre ne permet pas d'expliquer quelles espèces sont affectées, ce qui suggère que des facteurs autres que la lumière sont responsables de l'augmentation de la mortalité des semis sous cet arbuste. Nos résultats indiquent que la mortalité causée par la densité affecte quatre espèces, diminuant de ce fait la densité des semis à proximité des arbres parents. La dispersion, la mortalité liée à la densité et *R. maximum* agissent tous de façon à promouvoir ou limiter la coexistence des espèces, illustrant comment des facteurs multiples contrôlent la diversité des espèces.

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J. Hille Ris Lambers^{1,2} Department of Biology and Nicholas School of the Environment, Duke University, Durham, NC 27708, U.S.A.

J.S. Clark. Department of Biology, Duke University, Durham, NC 27708, U.S.A.

¹Corresponding author (e-mail: hille015@umn.edu).

²Present address: Ecology, Evolution and Behavior Department, University of Minnesota, St. Paul, MN 55108, U.S.A.

Introduction

Forest community structure and composition may be largely determined at early life history stages. Seeds represent the principal manner in which woody species colonize new habitats (Carter-Johnson 1988; Ribbens et al. 1994; Clark et al. 1998, 1999a). High mortality at seed and seedling stages (Cavers 1983; Jones and Sharitz 1998) further limit species' distributions (Clinton et al. 1994; Takahashi 1997; George and Bazzaz 1999a, 1999b; Kobe 1999; Beckage and Clark 2003). Because species vary greatly in their sensitivities to mortality agents at early life history stages, spatially variable environments profoundly affect

community composition of seedlings (Burton and Bazzaz 1991; Clark et al. 1998; Carlton and Bazzaz 1998; Kobe 1999; Beckage 2000).

Unfortunately, early life history stages are difficult to study. Estimates of dispersal that account for multiple seed sources under closed canopies are recent and therefore available from few sites (Ribbens et al. 1994; Clark et al. 1998, 1999a). Consequently, recruitment in natural forest communities has generally been studied in the absence of dispersal (Philips and Murdy 1985; Clinton and Vose 1996; Takahashi 1997; George and Bazzaz 1999a). High mortality of forest seeds and seedlings requires large sample sizes. Thus, studies tend to focus on a limited subset of the community (Carter-Johnson 1988; Clinton and Vose 1996; Cintra 1997; Wada and Ribbens 1997) or on just one of many processes that affect recruitment (Augsburger 1984; Clinton et al. 1994).

We develop a modeling framework that allows us to simultaneously quantify the effects of seed dispersal, the understory shrub *Rhododendron maximum*, and density-dependent mortality based on changes in spatial distributions across life history stages. We chose to study these three factors because all affect species at our sites and may affect forest structure. Few temperate tree species saturate the forest floor with seed, even when abundant (Ribbens et al. 1994; Clark et al. 1998, 1999a). This may limit interspecific competition and promote species diversity (Shmida and Ellner 1984; Clark and Ji 1995; Hurtt and Pacala 1995). Many temperate forest species experience strong density-dependent mortality at early life history stages (Streng et al. 1989; Jones et al. 1994; Packer and Clay 2000; Hille Ris Lambers et al. 2002), which can also promote species diversity (Janzen 1970; Connell 1971; Harms et al. 2000). Effects of both dispersal and density-dependent mortality may persist through adult stages (Plotkin et al. 2000). Finally, seedling densities of many species are depressed beneath *R. maximum* (Clinton et al. 1994; Clinton and Vose 1996; Beckage et al. 2000). The potential spread of *R. maximum* as a result of fire suppression and disturbance could therefore impact Southern Appalachian forest communities through its effects on seedling recruitment (Clinton et al. 1994; Clinton and Vose 1996).

We apply models to an extensive data set of adult tree, seed, seed bank, and seedling distributions collected from Southern Appalachian forests. We use a statistical approach that accommodates the effects of multiple processes on distributions that may operate simultaneously. Our approach allowed us to determine (i) the combined effects of seed dispersal, *R. maximum*, and density-dependent mortality on seed and seedling distributions and (ii) how species differences in seed size, abundance, and fecundity determine susceptibility to these influences. We expected that dispersal would most strongly limit seed distributions, while density-dependent mortality and *R. maximum* would become limiting at later life history stages. We expected that short dispersal distances for large-seeded species (Smith and Fretwell 1974; Clark et al. 1998) would result in more obvious dispersal patterns in local distributions than for small-seeded species. We also anticipated that low juvenile mortality of large-seeded species (Jurado and Westoby 1992; Greene and Johnson 1998) would allow dispersal patterns to persist to

later life history stages than for small-seeded species. Large-seeded species are generally more shade tolerant than small-seeded species (Leishman and Westoby 1994; Saverimuttu and Westoby 1996). Thus, we expected these species to be less affected by low light levels under *R. maximum* (Clinton and Vose 1996; Beckage et al. 2000) than small-seeded species. We further predicted that species having abundant seed (due to high fecundity, abundant parent plants, or both) are more likely to experience high density-dependent mortality due to high seed densities, which are more likely to attract host-specific seed predators or pathogens or cause intense intraspecific competition.

Conceptual framework

Fecundity and dispersal determine seed availability in the Southern Appalachians (Clark et al. 1998). We expected that distributions of later life history stages would be further modified by the effects of understory shrubs and density-dependent mortality (Fig. 1). We quantified these impacts by combining field data with a modeling approach. We determined the distributions of adult trees and of four early life history stages: s_0 , seed rain, s_1 , seed bank, s_2 , first-year seedlings; s_3 , older than first-year seedlings. These distributions were used to select among models that assume the effects of seed dispersal, the understory shrub *R. maximum*, and density-dependent mortality. We documented the progressive effects of each factor by determining how well these different models explained distributions of four consecutive early life history stages. We tested six models corresponding to these factors acting singly and in combination:

- (1) M-1 null model: neither dispersal, *R. maximum*, nor density-dependent mortality affects distributions of seeds, seed banks, or seedlings.
- (2) M-2 shrub effects: *R. maximum* determines spatial distributions of seed bank and seedling stages.
- (3) M-3 seed dispersal: spatial distributions of seed rain, seed bank, and seedling stages are determined by dispersal.
- (4) M-4 dispersal plus understory shrubs: seed dispersal patterns are altered in later life history stages by *R. maximum*.
- (5) M-5 dispersal plus density-dependent mortality: seed dispersal patterns are altered in later life history stages (seed bank and seedlings) by density-dependent mortality.
- (6) M-6 dispersal plus understory shrubs plus density-dependent mortality: seed dispersal patterns are altered in later life history stages by both *R. maximum* and density-dependent mortality.

These models are designed to assess the interactions among factors that operate progressively.

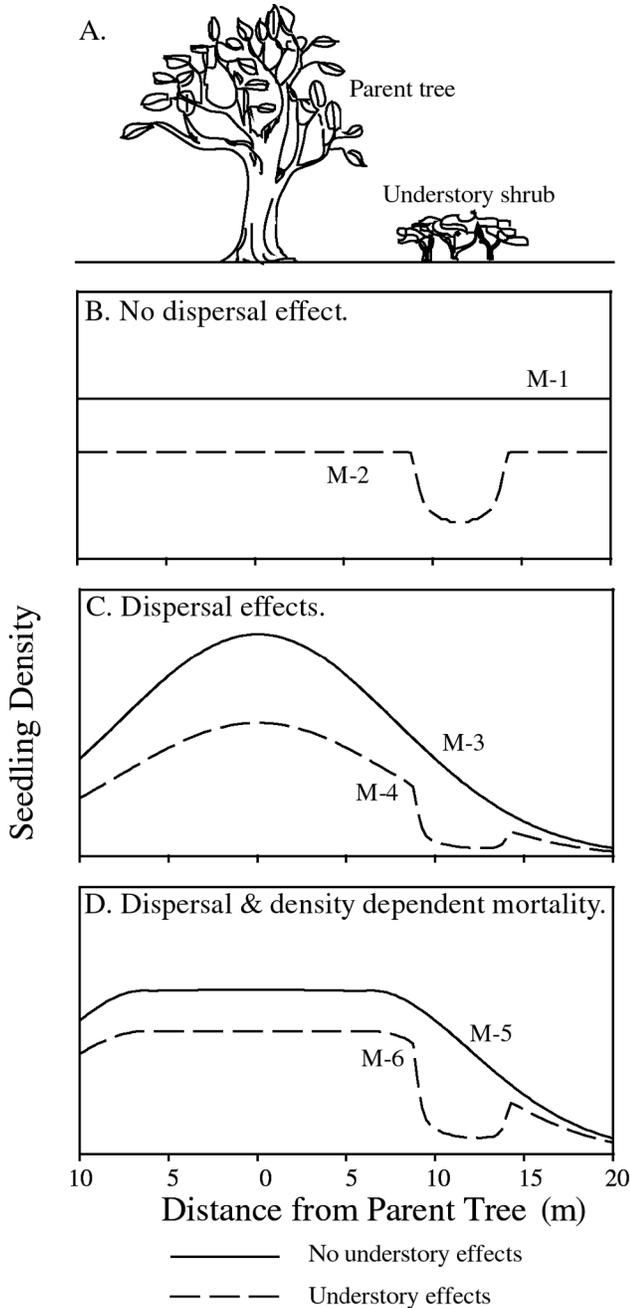
Our basic model for the spatial pattern of recruitment is

$$[1] \quad s_{kj} = v_k f(c_j) s_{0j}$$

where s_{kj} is the density of life history stage k at location j , v_k is the product of seed viability and mortality from seed to stage k (a fraction), $f(c_j)$ are the effects of understory shrubs (determined by cover c_j), and s_{0j} is seed input to location j , potentially modified by density-dependent mortality.

A null model follows directly from eq. 1 and is expected to best describe distributions for species with abundant adults, having broadly dispersed seed, and being insensitive

Fig. 1. Six conceptual models of how dispersal, understory shrubs, and density-dependent mortality can interact to control recruit densities. (A) Placement of parent trees and understory shrubs; (B–D) solid and broken lines indicate juvenile densities (offset to help distinguish between the lines). In Fig. 1B, juvenile distributions do not show effects of dispersal. If juvenile densities are determined by dispersal (as in Fig. 1C), they can subsequently be altered (as in Fig. 1D) by density-dependent mortality. In Figs. 1B–1D, solid lines are distributions not affected by understory shrubs and broken lines are those negatively affected by understory shrubs.



to the understory shrub *R. maximum* (M-1 in Fig. 1B). If the null model applies, dispersal and understory shrubs do not explain more of the variation in spatial pattern than does the

mean density (individuals per square metre) at stage k . This mean density is the product of seed input and the probability of surviving to stage k , v_k ,

$$[2] \quad s_{kj} = v_k \bar{s}_0$$

where \bar{s}_0 is the product of average basal area (\bar{b}) and fecundity (F , seeds per square metre of basal area per year).

M-2 describes the case where species having broadly dispersed seed or abundant adults are affected by understory shrubs (M-2 in Fig. 1B). Life history stages following seed dispersal will be randomly distributed across the forest floor, except under *R. maximum*. We assumed a proportionate decrease r in recruit density with increasing *Rhododendron* cover (leaf area) c_j :

$$[3] \quad f(c_j) = e^{-rc_j}$$

yielding the model

$$[4] \quad s_{kj} = v_k f(c_j) \bar{s}_0$$

Absence of understory effects are described by $r = 0$, i.e., the null model.

If spatial patterns are governed by dispersal (M-3 in Fig. 1C), seed distributions established by dispersal (distributions described by s_0) persist across subsequent life history stages (M-3 in Fig. 1C). We chose a two-dimensional Gaussian dispersal kernel (as in Clark et al. 1998) to parameterize initial distributions:

$$[5] \quad g(x_{ij}; d_0) = \frac{1}{\pi d_0} e^{-(x_{ij}/d_0)^2}$$

This kernel has one fitted parameter (d_0), the root mean square dispersal distance; x_{ij} is the distance from the i th parent to recruits at location j (seeds, seed banks, or seedlings per square metre). Seed density at location j is the sum of seed shadows

$$[6] \quad s_{0j} = \sum_{i=1}^m Fb_i g(x_{ij}; d_0)$$

where Fb_i is seed production of the i th tree and m is the number of trees that contribute seed to location j . Large values of d_0 in eq. 6 reflect broad dispersal. If dispersal effects persist across life history stages, then the distribution of stage k is equal to the initial seed distribution scaled by density-independent survival:

$$[7] \quad s_{kj} = v_k s_{0j}$$

An interaction of dispersal with understory shrubs results in seed shadows that are depressed in areas with high understory cover but otherwise retain initial dispersal patterns (M-4 in Fig. 1C). Recruit density is a function of both dispersal (as in eq. 7) and understory cover (eq. 4):

$$[8] \quad s_{kj} = v_k f(c_j) s_{0j}$$

Joint dispersal and density-dependent mortality (M-5) results in patterns that reflect initial distributions as subsequently modified by density-dependent mortality (M-5 in Fig. 1D). With density-dependent mortality, mortality at seed bank and seedling stages is greater at high densities of

conspecifics, either adult or juvenile. Because high seed densities occur close to the parent plant, we can infer density-dependent mortality from values of d_k that increase across subsequent life history stages because mortality is greater close to adult trees or at high densities of juveniles (Fig. 1D). Note that density-dependent mortality can result from specialist predators and pathogens (so-called Janzen–Connell effects; Janzen 1970 and Connell 1971) or from intraspecific competition; our models do not distinguish between these different processes. Equation 1 is used to test for these interactions by comparing how spatial distributions change from one life history stage to the next. Equation 7 or 8 is fitted to spatial patterns in recruitment for stage k . Increasing dispersal parameters across life history stages, i.e., $d_k > d_0$, suggest negative density-dependent mortality.

When density-dependent mortality interacts with both dispersal and understory shrubs (M-6 in Fig. 1D), seed bank or seedling densities, determined by seed dispersal (eq. 1), are subsequently modified by understory shrubs ($r > 0$) and density-dependent mortality ($d_k > d_0$). The result is juvenile densities that are lower under *R. maximum* and less concentrated around parent trees.

Study area

Our study site lies within the Coweeta Hydrologic Laboratory in the Southern Appalachians of western North Carolina (35°03'N, 83°27'W; Swank and Crossley 1988). Average monthly temperatures vary from 3°C in January to 22°C in July (Swift et al. 1988). Average rainfall ranges from 110 mm in October to 200 mm in March (Swift et al. 1988). Increasing elevation (which ranges from 600 to 1400 m) causes decreasing temperatures and increasing moisture (Swift et al. 1988). Soils are immature Inceptisols and well-developed Ultisols.

Forests have remained relatively undisturbed in the last 70 years. There are reports of burning by the Cherokee Indians and early European settlers in the 1800s (Douglas and Hoover 1988). Around that same time, limited agriculture and grazing impacted lower elevation forests. Selective logging occurred after the purchase of Coweeta basin by the U.S. Department of Agriculture in the early 1900s (Douglass and Hoover 1988). The last major disturbance was the chestnut blight in the 1930s, which (together with subsequent salvage logging of the American chestnut) removed *Castanea dentata*, an overstory dominant.

Temperate deciduous forests of the region host high tree diversity, and composition varies along environmental gradients (Whittaker 1956; Day et al. 1988). At lower elevations (<800 m), mesic coves support *Betula lenta*, *Magnolia fraserii*, and *Liriodendron tulipifera*. Along xeric ridges, *Pinus rigida*, *Quercus velutina*, and *Sassafras albidum* are abundant. At low to middle elevations, *Acer rubrum*, *Carya glabra*, *Nyssa sylvatica*, *Oxydendrum arboreum*, *Quercus prinus*, and *Quercus rubra* are canopy dominants. Upper elevations (>1200 m) are dominated by northern hardwood species, including *Acer pennsylvanicum*, *Acer saccharum*, *Betula alleghaniensis*, *Fagus grandifolia*, *Tilia americana*, and *Tsuga canadensis* (Day et al. 1988).

Rhododendron maximum is an ericaceous shrub that can dominate the understory except on xeric ridges (Day et al.

1988). *Rhododendron maximum* decreases light, moisture, and pH and has been shown to depress tree seedling densities (Monk et al. 1985; Philips and Murdy 1985; Clinton and Vose 1996; Beckage et al. 2000). *Rhododendron maximum* may be increasing in abundance in response to fire suppression and chestnut decline (Day et al. 1988; but see Woods and Shands 1959), potentially affecting forest composition by decreasing recruitment.

Materials and methods

Census data

Spatial relationships among adult trees, seed rain, seed bank, and seedling densities were measured on five permanent 80 × 80 m plots established in 1991. Sites represent common forest communities in the Southern Appalachians (Whittaker 1956): one in a mesic cove, one on a xeric ridge, two in mixed-oak communities, and one at high elevations in northern hardwoods. All trees greater than 2 m in height (including *Vitis* vines) were identified and mapped in plots in 1991. Diameters (at 1.43 m height) of mapped trees were measured in 1998. Adult tree mortality between 1991 (when the stands were first mapped) and 1998 was low in these stands (<1% annually) and biased towards small size classes (most <10 cm in diameter) with low fecundity. Seed survival in soil and seedling survival (J. Hille Ris Lambers, unpublished data) are low for all species, so that seeds in seed banks and seedlings censused between 1995 and 1999 almost certainly originated from living trees censused between 1991 and 1998.

Twenty 42 × 42 cm seed traps were established in each plot in 1991 and monitored from 1991 to 1998. Seed traps are lined with mosquito mesh to capture seeds, and mesh diameter was small enough to capture seeds of all species in this study except *R. maximum*. For this species, counts of seed capsules instead of seeds were used to parameterize seed rain dispersal patterns. To deter rodent seed predators, seed traps are covered with wire mesh (1.5 in. in diameter) and fixed 1.5 m above the ground (Clark et al. 1998). Efficiency trials indicated that seeds did not generally bounce off the wire mesh; over 85% of larger seeds (*Quercus* spp., *Carya* spp.) and 95% of smaller seeds (*Betula* spp., *Acer* spp.) dropped from 15 m above entered the seed trap (Clark et al. 1998). Three to four times annually, seeds and seed capsules from seed traps were sorted, identified to species (e.g., *R. maximum*, *L. tulipifera*, *Fraxinus americana*, *N. sylvatica*) or genus (e.g., *Acer* spp., *Betula* spp., *Quercus* spp.), and archived. Because the species within the genera dominate different stands (*Acer* spp., *Betula* spp.) or have similar fecundities (*Quercus* spp.), our lumping of species in this manner is unlikely to affect dispersal estimates.

Seed bank densities were sampled in August of 1995, 1996, 1997, and 1998 in all but one plot, which was sampled only in 1997 and 1998. Ninety percent of seed germination occurs before July at these sites (J. Hille Ris Lambers, unpublished data), and most seed banking species (except *A. rubrum*) set seed in autumn (Burns and Honkala 1990). Thus, sampling in August captures seeds that have survived in the soil at least 1 year (Thompson and Grime 1979).

The density of seedlings emerging from soil cores is an estimate of viable seeds in the soil. In each of the five plots,

Table 1. Hypothesized effects and basis for model selection.

Effects	Parameter vector \mathbf{p}	Model lacking effect ("null")	Criterion for rejection of null
1. Nonspatial null	Fv_k		
2. Shrub effects	Fv_k, r	1	$r > 0$
3. Dispersal	Fv_k, d_0	1	$d_k < \infty$
4. Dispersal + shrub effects	Fv_k, d_0, r	2 or 3	$d_k < \infty, r > 0$
5. Dispersal + density-dependent mortality	Fv_k, d_k	3 (d_0 from seed rain)	$d_0 < d_k < \infty$
6. Dispersal + density-dependent mortality + shrub effects	Fv_k, d_k, r	2, 4, or 5	$d_0 < d_k < \infty, r > 0$

Note: F , fecundity parameter (seeds per square metre basal area per year); v_k , product of seed viability and survivorship to stage k ; d_0, d_k , dispersal parameter (metres) fit to seed rain (0) or stage k ; r , mortality parameter (per unit leaf area index) due to *Rhododendron maximum*.

we removed 66 soil cores, 7.5 cm in diameter and 5 cm deep, from a 4-m grid within a 20 × 40 m area (1995, 1997, 1998). We removed an additional soil core adjacent to each seed trap in 1997 and 1998 for a total of 86 cores per stand in those years. A total area of 1.05 m² was thus sampled per plot, a high sampling area relative to other seed bank studies (Clark et al. 1999b). Given high densities of seeds in the soil (>15 seeds·m⁻² for most species), this sampling intensity adequately captures the spatial distribution of seed bank densities.

Soil cores were stratified at 4°C for 6 weeks. Roots and leaves were removed and the remaining material was spread 2 cm deep over sterile potting soil. Pots were placed in the greenhouse at 25°C with natural lighting and watered daily. Seedlings were identified as they emerged (censuses bi-monthly) and censuses continued for 8 months.

To quantify the spatial distribution of first-year and older than first-year seedlings, we censused all seedlings ≤0.25 m tall in July of 1996, 1997, and 1998 in eighty-six 1-m² quadrats adjacent to all seed bank sample points. Seedlings were separated into first-year and older than first-year age-classes on the basis of cotyledon presence-absence and stem woodiness. First-year seedlings are unambiguously identified by cotyledons, and few individuals reach older than first-year seedling stages, as seedling mortality is high for most species (J. Hille Ris Lambers, unpublished data). Seedlings were seldom counted more than once over the 3-year study period.

Seed traps, seedling quadrats, and sites of seed bank sampling were all well within the 80 × 80 m plot (>15 m from the edge, on average 25 m from the edge). Previous studies have shown that fecundity and dispersal parameter estimates converge at plot sizes (and distances from seed traps) much smaller than the size we used in this study (Clark et al. 1998, 1999b).

Rhododendron maximum leaf area index was determined at 167 locations in 1997 (at each seed bank and seedling sampling site and on a 10-m grid throughout the rest of each plot). At each location, leaf area index was obtained by averaging the number of leaves intercepting a 3-m vertical pole at the four corners of the 1-m² seedling quadrat.

Data modeling

We applied an inverse-modeling approach to quantify the effects of dispersal (similar to Ribbens et al. 1994; Clark et

al. 1998, 1999a), understory shrubs, and density-dependent mortality. The models assume spatial relationships between parent trees and juveniles outlined in Fig. 1. A negative binomial sampling distribution (NB) is the basis for the likelihood for n samples of life history stage k :

$$[9] \quad L_k = \prod_{j=1}^n \text{NB}[\hat{s}_{kj}(\mathbf{p}), \theta]$$

where \hat{s}_{kj} is the expected number of stage k recruits (seed rain, seed bank, or seedlings) in sample j depending on the vector of parameters \mathbf{p} specific to a given model (Table 1) and θ is a dimensionless shape parameter. We report parameter values describing dispersal (d_k), effects of *R. maximum* (r), and the composite coefficient Fv_k . Because fecundity (F), seed viability, and density-independent mortality (v_k) probably differ between plots, we fit the composite coefficient Fv_k separately for each plot.

For each species, seed, seed bank, or seedling densities were averaged at each sampling location across years. Plots having too few individuals over the entire study period to adequately fit models (less than two seed traps, soil cores, or seedling quadrats colonized for a particular species) were not included. We fit models to all four life history stages for each species and selected best-fitting models based on likelihood ratio tests or Akaike's information criterion (for non-nested models). The null model is nested within all other models ($d \rightarrow \infty$ and (or) $r \rightarrow 0$). With the exception of the nonnested pair 2 versus 3, effects were assessed with likelihood ratio tests against the model lacking that effect (Table 1).

Results

Parameter estimation and model selection

We examine community-wide patterns using all 20 species with at least one life history stage with sufficient densities to parameterize models (species in Table 2; Figs. 2 and 5). However, we only present model results for the 10 species whose seed, seed bank, or seedling distributions reflect effects of dispersal, *R. maximum*, or density-dependent mortality at more than one life history stage (species in Table 3). These species were *A. rubrum*, *A. pennsylvanicum*, *Betula* spp. (*B. allegheniensis* and *B. lenta*), *F. americana*, *L. tulipifera*, *N. sylvatica*, *Q. prinus*, *Q. rubra*, *R. max-*

Table 2. Life history characteristics (life form, successional status, shade tolerance, seed size, dispersal vector) of the 20 species used in this study.

Species	Life form ^a	Successional status ^a	Shade tolerant ^a	Seed size (g)	Dispersal vector ^a
<i>Acer pennsylvanicum</i>	Understory tree	Late	Yes	0.0358 ^a	Wind
<i>Acer rubrum</i>	Canopy tree	Early	Yes	0.0408 ^b	Wind
<i>Amalanchier laevis</i>	Understory tree	Unknown	Unknown	0.0084 ^c	Bird
<i>Betula allegheniensis</i>	Canopy tree	Mid to late	Intermediate	0.0101 ^a	Wind
<i>Betula lenta</i>	Canopy tree	Mid to late	No	0.0073 ^a	Wind
<i>Carya ovata</i>	Canopy tree	Late	Intermediate	3.0300 ^a	Mammal
<i>Cornus florida</i>	Understory tree	Unknown	Yes	0.1008 ^a	Bird
<i>Fraxinus americana</i>	Canopy tree	Late	Intermediate	0.0026 ^c	Wind
<i>Liriodendron tulipifera</i>	Canopy tree	Early	No	0.0363 ^a	Wind
<i>Oxydendrum arboreum</i>	Canopy tree	Mid	Yes	0.0001 ^a	Wind
<i>Nyssa sylvatica</i>	Canopy tree	Mid	Yes	0.1232 ^c	Bird
<i>Pinus rigida</i>	Canopy tree	Late	No	0.0072 ^a	Wind
<i>Quercus prinus</i>	Canopy tree	Late	Intermediate	4.545 ^d	Bird, mammal
<i>Quercus rubra</i>	Canopy tree	Late	Intermediate	4.774 ^c	Bird, mammal
<i>Quercus velutina</i>	Canopy tree	Late	Intermediate	1.855 ^d	Bird, mammal
<i>Rhododendron maximum</i>	Shrub	Unknown	Yes	0.0001 ^d	Wind
<i>Robinia pseudoacacia</i>	Canopy tree	Early	No	0.0189 ^a	Bird
<i>Sassafras albidum</i>	Understory tree	Early	No	0.0909 ^a	Bird
<i>Tilia americana</i>	Canopy tree	Late	Yes	0.0873 ^a	Wind
<i>Tsuga canadensis</i>	Canopy tree	Late	Yes	0.0091 ^a	Wind
<i>Vitis</i> sp.	Vine	Unknown	No	0.0333 ^d	Bird

^aBurns and Honkala (1990).^bField-collected seeds.^cData from the National Tree Seed Laboratory.^dYoung and Young (1992).

imum, and *Vitis* sp. Collectively, these species make up over 70% of the trees found in our plots (by basal area). They also represent a diversity of life history strategies (Table 2) in terms of dispersal vector (wind, mammals, and birds), growth form (canopy tree, understory tree, shrub, and vine), and successional status (early and late).

Most of the other 19 woody perennial species in permanent plots had low recruitment over the study period, and sample sizes were insufficient to fit models to spatial distributions of juveniles. Seed, seed bank, and seedling densities were too low to parameterize models for nine taxa (*A. saccharum*, *Acer spicatum*, *F. grandifolia*, *Hammamelis virginiana*, *Ilex opaca*, *Magnolia acuminata*, *M. fraserii*, *Quercus alba*, *Quercus marilandica*), and we do not include or interpret results for these taxa in this paper. Six taxa had sufficiently high seed densities to parameterize dispersal models but too few individuals at seed bank or seedling stages to track effects of dispersal, density-dependent mortality, and *R. maximum* over time (*Carya* spp., *Cornus florida*, *Oxydendrum arborea*, *P. rigida*, *T. americana*, *T. canadensis*). Four taxa had sufficient densities to parameterize models at seed or seedling stages, but we were unable to reject the null model (no effects of dispersal, *R. maximum*, and density-dependent mortality on spatial distributions) for any life history stage (*Amelanchier laevis*, *Q. velutina*, *Robinia pseudoacacia*, *S. albidum*).

Effects of dispersal, *R. maximum*, and density-dependent mortality

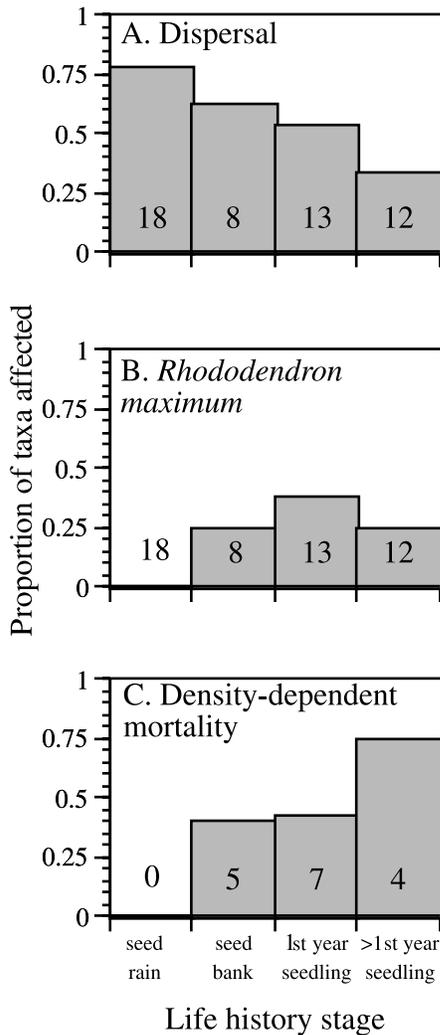
Seed dispersal patterns tended to dissipate at later life history stages, while spatial distributions suggest that the ef-

fects of *R. maximum* and density-dependent mortality increased from the time of dispersal through seedling stages (Fig. 2; Table 3). Simultaneous effects of dispersal, *R. maximum*, and density-dependent mortality (M-4 through M-6) were primarily found at later life history stages. In only a few cases were later life history stages solely affected by dispersal or *R. maximum* (*Betula* spp., *F. americana*, *R. maximum*) (Table 3).

The persistence of spatial distributions laid down by seed dispersal are evident from dispersal models (M-3 through M-6) that best explained distributions of more than half of the taxa tested at all life history stages (Fig. 2A). For example, *L. tulipifera* adults are clustered in the south corner of our cove site (Fig. 3A). Seed banks and first-year seedlings (densities represented by small boxes in Figs. 3C and 3D) follow the same initial distribution established by seed dispersal (Fig. 3B). However, dispersal patterns of many species dissipate with age. Fewer species show evidence of dispersal at older than first-year seedling stages (three taxa) than at seed rain stages (18 taxa, eight not shown in Table 3; Fig. 2A). A comparison of patterns across life history stages within a species supported our expectation that dispersal patterns would dissipate in a predictable fashion. When a dispersal effect was absent at one life history stage, it was also absent at all later life history stages (Table 3), with the exception of *N. sylvatica*.

Rhododendron maximum depressed seed bank or seedling densities of *A. pennsylvanicum*, *A. rubrum*, *F. americana*, *Q. rubra*, and *Vitis* sp. (Fig. 2B; Table 3). For example, *A. rubrum* first- and older than first-year seedling densities are high near openings in the *Rhododendron* canopy (Fig. 4).

Fig. 2. Effects of seed dispersal, *Rhododendron maximum*, and density-dependent mortality on spatial distributions of different life history stages. The height of the shaded bars indicates the proportion of taxa for which (A) dispersal, (B) *R. maximum*, and (C) density-dependent mortality affected spatial distributions of seeds (dispersed or in the seed bank) or seedlings (first year or older than first year). The number within each bar represents the total number of taxa for which sample sizes were large enough to fit models.



The effect of *R. maximum* persisted at later life history stages; if recruit densities were depressed under *R. maximum* at one life history stage, later life history stages were also depressed (Table 3). Mortality due to *R. maximum*, as represented by the parameter *r*, generally increased at later life history stages (Table 3).

Our results suggest that the proportion of taxa undergoing density-dependent processes increased at later life history stages (Fig. 2C). For *A. rubrum*, *N. sylvatica*, *Q. rubra*, and *Vitis* sp., dispersal parameters for seed bank and (or) seedling densities were greater than those for seed rain (Table 3), indicating that juveniles were less concentrated around parent trees at later life history stages. *Liriodendron tulipifera* dispersal parameters decreased across life history stages, indicating that seed or seedling survival was greater near adult trees.

Correlates of seed size and dispersal vector

Seed size was generally not a good predictor of whether seed dispersal patterns were maintained over time (no relationship between seed size and whether dispersal models fit seed or seedling distributions as tested by logistic regression). However, dispersal patterns were generally less obvious for animal-dispersed species than for wind-dispersed species (Fig. 5). M-3 through M-6 (those including effects of dispersal) provided a good fit to all wind-dispersed species having recruits at seed rain and seed bank stages (Fig. 5A) and for greater than half of wind-dispersed species with recruits at seedling stages. Less than half of animal-dispersed species tested fit dispersal models well, with the exception of seed rain stages (Fig. 5B).

Both small-seeded (*F. americana*) and large-seeded species (*Q. rubra*) were affected by *R. maximum*. There was no relationship between seed weight and the magnitude of mortality associated with *R. maximum* (Pearson’s correlation between seed weight and *r* parameters is 0.05, with *P* = 0.80).

Density-dependent mortality affected taxa with both relatively low (e.g., *Q. rubra*) and high fecundities (e.g., *A. rubrum*). There was no relationship between average seed production and the magnitude of change in dispersal parameters across taxa. However, the two species with the highest densities of seedlings in our stands (due to abundant adults) were both affected by density-dependent mortality (*A. rubrum*, *Q. rubra*).

Estimation of dispersal and *R. maximum* effects

Interactions involving dispersal, *R. maximum*, and density-dependent mortality may alter estimates of both dispersal and understory effects. The effects of *R. maximum* were underestimated by as much as 70% when the effects of dispersal were ignored (comparing *r* parameters between M-2 and M-4 or M-6; results not shown). Density-dependent processes increase (or in one case, *L. tulipifera*, decrease) dispersal estimates at later life history stages in a species-specific manner (Table 3), with differences as large as 30 m (e.g., the *Q. rubra* dispersal parameter fitted to seed rain versus older than first-year seedlings).

Discussion

The inverse-modeling approach reveals the effects of seed dispersal on spatial distributions of tree species and how dispersal patterns are subsequently altered by *R. maximum* and density-dependent mortality. Seed distributions are determined by dispersal, while seedling distributions suggest limitation by a combination of dispersal, *R. maximum*, and density-dependent processes (Table 3). The relative effects of dispersal, *R. maximum*, and density-dependent mortality often depend on species characteristics such as seed size, dispersal vector, and local abundance. Finally, seed dispersal, *R. maximum*, and density-dependent mortality may strongly influence forest dynamics through their effects on seed and seedling dynamics.

Persistent dispersal effects

Recruitment of all tree species is limited by seed dispersal at early life history stages. Seeds and seedlings of most species are clumped near adult trees (Fig. 2; Table 3) (Clark et

Table 3. Seed or seedling production, mean dispersal distance, the effects of *Rhododendron maximum*, and probabilities (from likelihood ratio tests) of effects of seed dispersal, *R. maximum* mortality, and density-dependent mortality.

Taxon and life history stage	Seed or seedling production per unit basal area (Fv_k , $\text{cm}^{-2}\cdot\text{year}^{-1}$)	Mean dispersal distance (d_k , m)	<i>Rhododendron maximum</i> effects (r , leaf area index $^{-1}\cdot\text{year}^{-1}$)	Probability of no effect (likelihood ratio test)		
				Dispersal $P(d \text{ infinite})$	<i>Rhododendron maximum</i> $P(r = 0)$	Density-dependent mortality $P(d_k = d_0)$
<i>Acer pennsylvanicum</i>						
Seed rain	24.49	18.51	—	<0.01	ns	—
First-year seedling	0.4010	29.27	0.470	0.02	0.04	ns
Older than first-year seedling	0.3837	26.26	2.10	<0.01	<0.01	ns
<i>Acer rubrum</i>						
Seed rain	24.49	18.51	—	<0.01	ns	—
Seed bank	7.092	19.09	0.273	0.02	0.03	ns
First-year seedling	1.269	30.35	0.336	<0.01	<0.01	<0.01
Older than first-year seedling	0.3747	43.20	0.490	<0.01	<0.01	<0.01
<i>Betula</i> spp.						
Seed rain	1282	42.52	—	<0.01	ns	ns
Seed bank	391.2	42.82	0	<0.01	ns	—
First-year seedling	0.1926	∞	0	ns	ns	—
Older than first-year seedling	0.01196	∞	0	ns	ns	—
<i>Fraxinus americana</i>						
Seed rain	4.323	21.13	—	0.03	ns	—
First-year seedling	0.05146	∞	0.475	ns	0.02	—
<i>Liriodendron tulipifera</i>						
Seed rain	475.1	34.45	—	<0.01	ns	—
Seed bank	146.4	27.92	0	<0.01	ns	ns
First-year seedling	0.07932	12.26	0	<0.01	ns	<0.01
Older than first-year seedling	0.01156	∞	0	ns	ns	—
<i>Nyssa sylvatica</i>						
Seed rain	5.317	6.98	—	<0.01	ns	—
First-year seedling	0.006793	∞	0	ns	ns	—
Older than first-year seedling	0.02947	11.87	0	0.05	ns	0.02
<i>Quercus prinus</i>						
Seed rain	2.416	12.06	—	<0.01	ns	—
First-year seedling	0.02428	9.32	0	<0.01	ns	ns
Older than first-year seedling	0.007521	∞	0	ns	ns	—
<i>Quercus rubra</i>						
Seed rain	2.416	12.06	0	<0.01	ns	—
First-year seedling	0.04564	32.25	0.275	0.04	0.04	<0.01
Older than first-year seedling	0.1269	41.02	0.252	0.05	0.05	<0.01
<i>Rhododendron maximum</i>						
Seed rain	1355	6.51	—	<0.01	ns	—
Seed bank	0.3019	20.51	0	<0.01	ns	<0.01
First-year seedling	8.47×10^{-5}	8.17	0	0.02	ns	ns
<i>Vitis</i> sp.						
Seed rain	181.3	12.86	—	0.10	ns	—
Seed bank	1568	23.62	5.43	<0.01	<0.01	<0.01
First-year seedling	6.850	23.06	94.4	<0.01	0.02	<0.01

Note: d_k , the dispersal parameter fit to k = seed rain, seed bank, first-year seedling, and older than first-year seedling data; d_0 , the dispersal parameter fit to seed rain data; —, not applicable; ns, no significant effect ($P > 0.05$).

al. 1998). Although mortality is high and spatially variable (as a result of *R. maximum* and density-dependent mortality, among other factors; Table 3), dispersal still influences seedling distributions of six species more than 2 years after dispersal (Table 3). Other species (Table 2; species not discussed in this paper) are probably also limited by dispersal. They are at low densities within plots (affecting our

ability to fit dispersal models) or are dispersed by birds (e.g., *Amelanchier* spp., *R. pseudoacacia*, *S. albidum*), a process that is not well described by current dispersal models (Clark et al. 1999a).

Whether seed dispersal or mortality most limits distributions of later life history stages depends on the magnitude of mortality and on the scale at which agents of mortality oper-

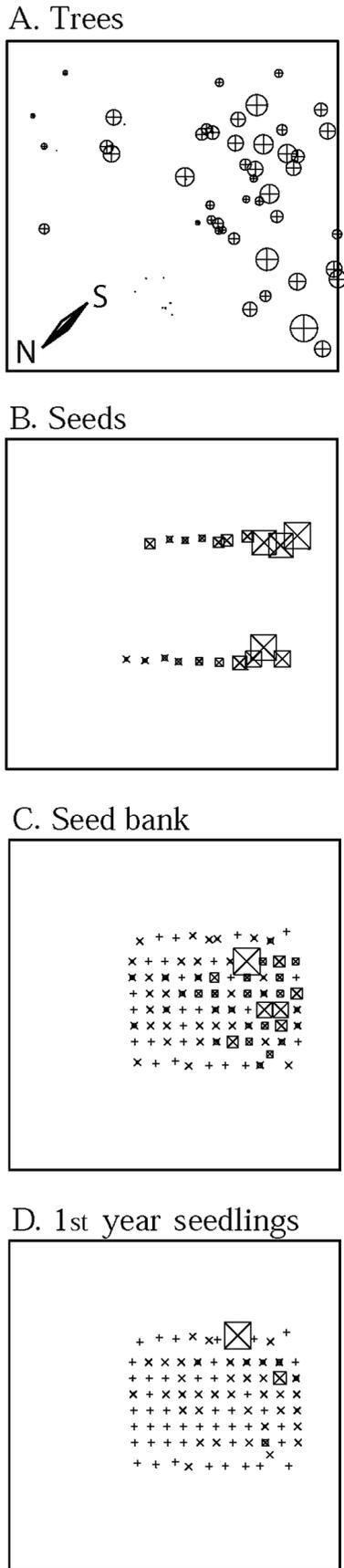
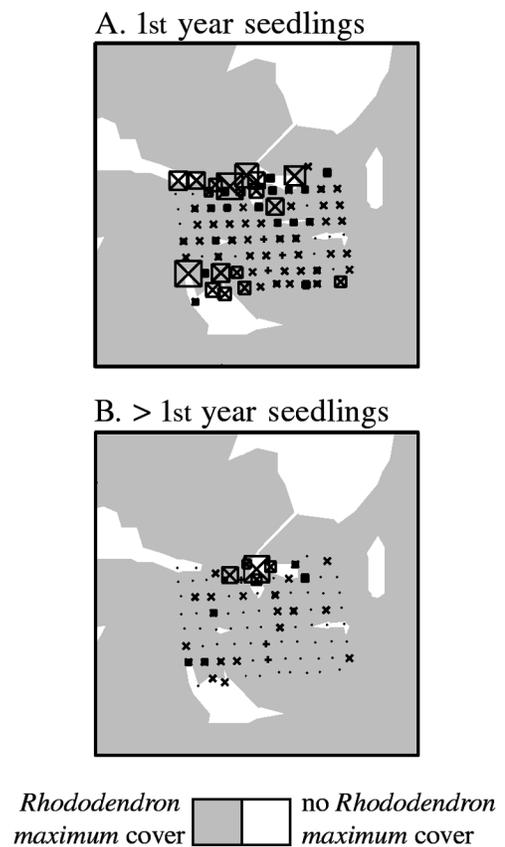


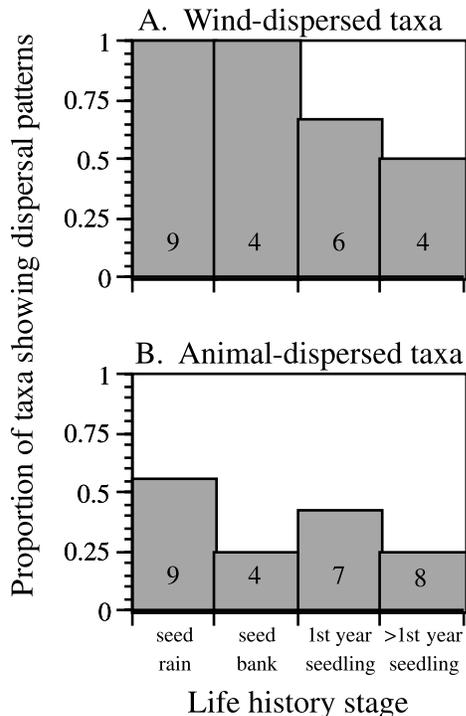
Fig. 3. Distribution of *Liriodendron tulipifera* (A) trees, (B) seeds, (C) seed banks, and (D) first-year seedlings at one of five plots. The largest box represents the border of the 80 × 80 m plot. Circles with crosses in Fig. 3A are locations of *L. tulipifera* trees, scaled in size to diameter. Small boxes or crosses in Figs. 3B–3D are locations of seed, seed bank, or seedling censusing and are scaled in size to seed rain, seed banks, or seedling densities at those locations.

Fig. 4. Distribution of *Acer rubrum* (A) first-year seedlings and (B) older than first-year seedlings at one of five plots. The largest box represents the border of the 80 × 80 m plot. Smaller boxes or crosses are locations of seedling censusing, scaled in size to relative seedling densities at those points. Points indicate zero seedlings. Shading indicates areas where *Rhododendron maximum* shrubs are found.



ate. *Betula* spp., for example, experience high mortality as a seedling (fewer than 3% of germinated seedlings survive for more than 3 months; J. Hille Ris Lambers, unpublished data). Average seed dispersal distances for *Betula* spp. are large (>40 m; Table 3) (Clark et al. 1998) compared with the scale at which light and moisture vary, both of which are important for survival and growth (Carlton and Bazzaz 1998). Dispersal models explain seed distributions well but not seedling distributions for birch (Table 3), suggesting that distribution of light gaps and high moisture microsites probably limit recruitment. In contrast, *Q. rubra* has high survival as a juvenile (35% of seedlings survive to the following growing season) and short dispersal distances (Ta-

Fig. 5. Persistence of seed dispersal patterns for (A) wind-dispersed and (B) animal-dispersed taxa. The height of the bars indicates the proportion of taxa for which spatial distributions of seeds (dispersed or in the seed bank) or seedlings (first year or older than first year) were significantly clustered around adult trees. The number within each bar represents the number of taxa for which models were fit.



ble 3). *Quercus rubra* seedling distributions are strongly influenced by seed dispersal, in spite of abundant adult trees and mortality due to both *R. maximum* and density-dependent mortality (Table 3).

We initially expected seed dispersal patterns of large-seeded taxa to more often persist across life history stages than those of small-seeded taxa because seed size is generally negatively correlated with seed dispersal distances but positively correlated with seedling survival. Seed and seedling distributions of *Betula* spp. (small-seeded) and *Q. rubra* (large-seeded) are consistent with this idea. In general, however, we did not find that seed size explained which species remain limited by dispersal at seedling stages. We found that dispersal patterns are more often retained by wind-dispersed taxa than animal-dispersed taxa (Fig. 5), indicating that the distribution of adult trees tends to determine seedling distributions of wind-dispersed taxa more often than seedling distributions of animal-dispersed taxa. Does this mean that large-seeded animal-dispersed taxa have a recruitment advantage over small-seeded wind-dispersed taxa in their ability to both colonize (due to secondary dispersal) and survive (due to greater seed reserves)? Not necessarily because large-seeded animal-dispersed species have lower seed production (Clark et al. 1998) and experience higher seed predation (Burns and Honkala 1990; Beckage 2000) than smaller-seeded wind-dispersed species.

Effects of *R. maximum*

Rhododendron maximum decreases seedling densities of many species in the Southern Appalachians (Table 3) (Clinton et al. 1994; Beckage et al. 2000). Seedling densities of at least four species were depressed from 25% (*Q. rubra*) to 99% (*Vitis* sp.) beneath *R. maximum* (Table 3). We suspect that many other species are negatively affected by *R. maximum* (e.g., *L. tulipifera* and *Q. prinus*; Beckage et al. 2000; Beckage and Clark 2003) but that low sample sizes prohibit us from detecting effects. Because our data only extend to second-year seedling stages, effects of *R. maximum* on later life history stages are uncertain but possibly more severe (Philips and Murdy 1985; Clinton et al. 1994; Baker and Van Lear 1998; Beckage et al. 2000).

Rhododendron maximum alters numerous environmental factors (light, moisture, pH, litter; Monk et al. 1985; Beckage 2000). The effects of *R. maximum* are first apparent at first-year seedling stages, suggesting that they are initially a result of reduced germination due to either low light or low moisture (Clinton and Vose 1996; Nilsen et al. 1999; Beckage et al. 2000). However, *R. maximum* continues to decrease seedling densities at later life history stages (parameter r increases; Table 3), suggesting additional effects on seedling survival (Beckage et al. 2000). Furthermore, seed size and shade tolerance do not predict which species are affected by *R. maximum*, indicating that increased mortality under this shrub is likely a result of more than simply reduced light.

Density-dependent mortality

Our analyses do not directly measure density-dependent mortality; rather, we infer density-dependent mortality from the changes in the spatial relationship between seeds, seed banks, and seedlings relative to adult trees (as reflected by increases in d_k across life history stages). However, we believe that these changes are most likely the result of the kind of density-dependent mortality that can promote species diversity (Janzen 1970; Connell 1971; Pacala and Crawley 1992; Webb and Peart 1999), either through the effects of host-specific agents (predators, pathogens) on dense patches of seeds or seedlings or through intraspecific competition that is more intense than interspecific competition. Spatial distributions of all life history stages were averaged across multiple years (seeds: 1992–1998, seed banks: 1995–1998, seedlings: 1996–1998), reducing the chance that annual variability (e.g., in wind speed) affected our estimates of dispersal. Also, previous work (Hille Ris Lambers et al. 2002) indicates that dominant species at these study sites (*A. pennsylvanicum*, *A. rubrum*, *Betula* spp., *F. americana*, *L. tulipifera*, *Q. rubra*) experience density-dependent mortality at early life history transitions.

We therefore feel that it is likely that density-dependent processes strongly limit recruitment of several species at Coweeta. The two species having highest seedling densities (*A. rubrum*, *Q. rubra*) experience changes in seedling distributions relative to seed distributions consistent with density-dependent mortality (Table 3) (Hille Ris Lambers et al. 2002). These effects are likely to extend beyond seedling stages, as the effects of density on mortality are strong: transition probabilities are as much as 70% lower when con-

specific seed is abundant. Our use of seed rain and seedling densities averaged across years results in a conservative estimate of density-dependent mortality because mortality is probably highest in years of high seed production. Thus, density-dependent mortality may affect more taxa than indicated by this study.

Dispersal parameters may decrease across life history stages for reasons other than density-dependent processes. Dispersal parameters of *L. tulipifera* decreased across life history stages (Table 3), indicating that seedlings are more concentrated around adult trees than seeds are (Fig. 2). This species grows faster and has greater survival in moist, high-light environments both as an adult tree and as a seedling (such as mesic coves; Burns and Honkala 1990). Thus, greater seed or seedling survival close to parent trees likely reflects microsite requirements of juveniles that are often found in areas where adult trees are abundant. This in turn leads to seedling distributions that are more concentrated around adult trees than seed distributions are.

The prevalence of density-dependent mortality in temperate deciduous forests has implications beyond our understanding of the forces that structure these forests. The Janzen–Connell model postulates that high species diversity in the tropics may be caused by high numbers of specialist predators and pathogens (Connell 1970; Janzen 1971; Clark and Clark 1984; Coley and Barone 1996; Givnish 1999; Harms et al. 2000). This hypothesis has remained largely untested because there are more studies of density-dependent mortality in the tropics than in temperate zones (e.g., Augspurger 1984; Clark and Clark 1984; Okuda et al. 1997; Webb and Peart 1999; Harms et al. 2000; but see Nakashizuka et al. 1995, Houle 1995; Packer and Clay 2000; Hille Ris Lambers et al. 2002). Our data suggest that the species that are most successful in temperate deciduous forests as seedlings (*A. rubrum*, *Q. rubra*) may be limited by density-dependent processes, which might include the effects of host-specific predators or intraspecific competition for resources. Thus, density-dependent mortality may be as important in temperate forests as in tropical forests, suggesting that its postulated association with the latitudinal gradient of species diversity be reconsidered.

Consequences of interacting processes

We found that seed dispersal, understory shrubs, and density-dependent mortality all affect seed or seedling distributions in ways that could influence the diversity of Southern Appalachian forests. Species with high seedling survival (J. Hille Ris Lambers, unpublished data) generally have limited dispersal (e.g., *Q. rubra*, *N. sylvatica*; Table 3) or low seed production (e.g., *R. pseudoacacia*, *S. albidum*; J.S. Clark, unpublished data) relative to species with low seedling survival (e.g., *Betula* spp., *Acer rubrum*; Table 3). Theory has shown that such a negative correlation between colonization and competitive ability can promote diversity (Shmida and Ellner 1984; Tilman 1990, 1994; Hurtt and Pacala 1995). Our results also suggest that the most abundant species at our sites experience density-dependent mortality. Such effects can increase species diversity by preventing common species from dominating forest communities, thus allowing more rare species to persist (Janzen

1970; Connell 1971; Pacala and Crowley 1992; Harms et al. 2000). *Rhododendron maximum* decreases diversity locally by reducing seedling densities of several species beneath it (Beckage et al. 2000) (Table 3).

We have come a long way towards understanding species diversity since Hutchinson (1961) first asked how so many plant species coexist on a few limiting resources. Ecologists have used theory to show that numerous processes can allow species to coexist (Janzen 1970; Connell 1971; Grubb 1977; Shmida and Ellner 1984; Pacala and Tilman 1994; Clark and Ji 1995; Hurtt and Pacala 1995). Empirical studies confirm that many of these processes operate in natural communities (e.g., Burton and Bazzaz 1991; Ribbens et al. 1994; Takashi 1997; George and Bazzaz 1999a, 1999b; Carlton and Bazzaz 1998; Clark et al. 1998; Harms et al. 2000; Packer and Clay 2000; Hille Ris Lambers et al. 2002). Our study demonstrates that species distributions are controlled by several processes operating at early life history stages. Although the notion of interactive effects is not a new one (Grubb 1977; Tilman 1990; Eriksson and Ehrlén 1992; Pacala and Rees 1998), our study is one of few to simultaneously quantify processes that all strongly affect seedling distributions and thus can affect community composition.

Conclusions

The interactions of dispersal, understory shrubs, and density-dependent mortality during early life history stages of Southern Appalachian trees affect seedling dynamics and thus may affect community structure. Dispersal limits recruitment of most species and, in spite of high mortality due to multiple limiting factors, continues to be a dominant force in determining seedling distributions. However, *R. maximum* and density-dependent mortality also affect seedling distributions and become more limiting over time. *Rhododendron maximum* decreases seedling densities of five species; thus, this shrub affects community composition locally. Recruitment of abundant species in the Southern Appalachians is likely limited by density-dependent mortality, suggesting that density-dependent mortality may be an important process promoting diversity in temperate as well as tropical forests. Finally, dispersal, understory shrubs, and density-dependent mortality interact to affect seed and seedling distributions, illustrating the importance of studying multiple processes to understand spatial distributions.

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