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Performance and population dynamics of a native understory herb differ between young and old forest stands in the Southern Appalachians

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ABSTRACT

Anthropogenic disturbances (e.g., logging) can strongly affect the composition and structure of forest understory herb communities, with land-use legacies often persisting for decades or even centuries. Many studies of forest plant response to land-use history have focused on species distributions and abundances, and argued broadly for either dispersal or establishment limitation as biological mechanisms for slow recolonization. We asked how performance and population dynamics of the temperate forest herb *Prosartes lanuginosa* differed between recently logged (20–40 years ago) and old (>90 years) logged forests in the Southern Appalachians, USA. All stands were well developed with canopy closure ranging from 59–90%. Performance of individual plants ($N = 859$) was monitored over three years across 19 forest stands ($N = 9$ recent and 10 old). We also conducted a seed sowing experiment to determine whether germination and establishment differed with stand age. Stage-based matrix models and life table response experiments (LTREs) were used to quantify the contributions of each life-history transition to observed differences in population growth rates (λ) across stands and between years. Field measurements revealed that population growth rates were higher in older logged stands ($\lambda = 0.78–0.84$) than in more recently logged stands ($\lambda = 0.68–0.74$), primarily because of reduced fecundity and reduced recruitment from vegetative to flowering life stages. Seed germination and seedling survival did not differ between old and young logged forests. Across stands, population growth rates were higher during the first annual transition than the second, which followed a drought spring. However, the mechanisms for these differences in λ varied with stand age; populations in old forests responded to drought conditions by lowering fecundity, whereas populations in young forests responded with lower recruitment from vegetative to flowering stages. Our results showed that logging history affects plant performance beyond the establishment phase and interacts with environmental conditions to influence population dynamics. Our results also emphasize the need for multiple performance measures to assess the effects of land-use history on forest plants.

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1. Introduction

The role of land-use history in determining the structure, composition, and population dynamics of forest plant communities is of long-standing interest to ecologists, particularly given the extent of deforestation followed by afforestation (both spontaneous and intended) in temperate landscapes (Flinn et al., 2005; Hermy and Verheyen, 2007). Old growth forests are especially rare in the US and Europe; more than half of the forest cover in the US is less than 60 years old (Gilliam, 2007), and different forms of land uses have relegated old-growth forests to small tracts of 4–40 hectares comprising only 0.09% of their original area (Davis, 1993).

Consequently, in addition to tree age and forest structure, the characteristics of forest understories often represent legacies of past land use, such as timber harvesting or farming. Forest herbs represent the majority of species diversity in temperate deciduous forests and are especially sensitive to disturbance across broad temporal and spatial scales (Gilliam, 2007). Because many species of forest herbs have qualities that make them poor dispersers, including large seeds, low fecundity, and ant-mediated dispersal (Hermy et al., 1999; Hermy and Verheyen, 2007; Matlack, 1994), they must adapt fairly rapidly to changing conditions or face local extinction.

Variation in the pattern of forest plant species distributions due to intensity of historic land use (including past agriculture and/or logging) has been well documented, and includes reduced species richness, cover, and abundance of herbs (Bellemare et al., 2002; Pearson et al., 1998; Singleton et al., 2001; Vellend, 2005; Wyatt

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and Silman, 2010), reduced heterogeneity of herb species (Fraterrigo et al., 2006), altered spatial structure of herb populations including higher density of small non-flowering plants in young forests (Jenkins, 2009), increased cover of invasive species (Kuhman et al., 2011) and decoupled relationships among herb diversity, stand structure, and soil nutrients (Gilliam, 2002; Vellend et al., 2007). Schulte et al. (2007) found that in the northern-central US, secondary forests have lower species diversity, functional diversity, and structural complexity compared to pre-Euro-American forests. While many studies have focused specifically on the effects of agricultural history (including persistent loss of forest cover) on forest herbs (Dupouey et al., 2002; Hermy, 1994; Motzkin et al., 1996; Peterken, 1984), others have found that the effects of logging alone on the forest understory can last for decades or even centuries (Duffy and Meier, 1992; Elliott et al., 1997; Meier et al., 1995; Wyatt and Silman, 2010). Logging continues to be a dominant form of land use in the Southern Appalachians (USA), perpetuating a long-term debate over the impacts of logging on forest herbs.

Although few studies have examined the mechanisms that restrict certain species to primary forests, most argue broadly for limitation either by dispersal (seed availability) or establishment. Following a disturbance, dispersal and establishment act as a series of ecological filters. A dispersal filter, including dispersal mechanism, existence of a seed bank, and distance to the nearest seed source, determines which species are most likely to have propagules reach the site. Subsequently, abiotic and biotic establishment filters affect the success of germination and seedling survival (Clark et al., 1998). Seed germination experiments often reveal higher or similar germination rates in secondary vs. primary forests (Graae et al., 2004; Vellend et al., 2000; Verheyen and Hermy, 2004), implying that dispersal may be more limiting than establishment. However, in meta-analyses, Turnbull et al. (2000) and Clark et al. (2007) suggested that establishment limitation plays a stronger role in limiting recruitment for many species. Dispersal and establishment hypotheses are not mutually exclusive (Clark et al., 2007; Eriksson and Ehrlen, 1992; Vellend, 2005), and little is known about the fate of forest plants once they do recolonize secondary forests (Baeten et al., 2009). Of course, the trajectory of vegetation recovery following human disturbance, including the relative influence of dispersal and establishment limitation, will depend on the characteristics of the disturbance, the extent to which the environment and resource availability are modified, and the abilities of plant species to survive or recolonize (Peters et al., 2011).

Many studies that have examined the response of the herb layer to anthropogenic disturbance have focused solely on species distributions and abundances. Studies in which multiple aspects of life-history are evaluated for populations in both old and young forests are rare (Donohue et al., 2000; Holt et al., 1995, but see Bruna, 2003; Bruna and Oli, 2005; Farrington et al., 2009; Jacquemyn and Brys, 2008). Species abundance patterns alone are not sufficient to discern whether current environmental conditions provide suitable habitat, as populations are rarely in an equilibrium state, particularly in recently disturbed sites (Valverde and Silvertown, 1998), nor are germination rates sufficient without information on seedling recruitment to subsequent life stages. Indeed, patterns of distribution and abundance at one point in time may mistake the results of ongoing processes for those of stable conditions (Bruna and Oli, 2005).

Measures of plant performance (e.g., growth, reproduction, mortality) can be more informative than measures of distribution or abundance for assessing the regional status of a species. Because plant populations take time to respond to changing environmental conditions, performance indicators can be a step ahead of distribution measures, and can help forecast the future status of a population. Although performance measures by themselves can be highly variable (Valverde and Silvertown, 1998), in the context of a species' entire life history, subtle changes in performance can be very important. Thus, comprehensive demographic data are needed to focus management toward appropriate targets, such as mitigating population declines that are driven by increased mortality versus reduced fecundity, germination, or other demographic drivers. Life Table Response Experiments (LTRE) and elasticity analyses can provide important insight into the different mechanisms responsible for altered plant performance related to land-use history (Bruna and Oli, 2005; Caswell, 2001).

Here, we use field measurements and LTRE analyses to investigate the effects of logging history on population dynamics of *Prosartes lanuginosa*, a forest understory herb characteristic of primary forests without intensive land-use history (Ford et al., 2000; Mitchell et al., 2002; S. Pearson, unpublished data). We also conducted seed-sowing experiments in sites where *P. lanuginosa* was present and in sites where it was absent. We asked how projected rates of population growth (λ), seed germination and establishment, and stage structure of *P. lanuginosa* differed between forest stands >90 years ago (''old'') and stands logged between 20 and 40 years ago (''young'') and across years with different patterns of temperature and precipitation. In addition, we quantified the contributions of each life-history transition to observed differences in λ across stands as well as years. We hypothesized that: (i) projected population growth rates would be higher in old stands, (ii) populations would show some evidence of dispersal limitation; thus germination of experimentally sown seeds would be equal across old and young stands and in sites where the focal species was both present and absent prior to seed-sowing, and (iii) that the stage structure of *P. lanuginosa* populations would differ more from the stable stage distribution in young stands because these populations are less mature and would likely contain fewer large, flowering individuals.

2. Methods

2.1. Study area

The study was conducted in the French Broad River Basin in Buncombe and Madison Counties of western North Carolina, USA (Fig. 1). The study region lies within the Southern Blue Ridge physiographic province, which is characterized by steep terrain and mixed-mesophytic deciduous forest (Braun, 1950). This area receives on average 125 cm of precipitation per year with mean winter temperatures of 4 °C and mean summer temperatures of 23 °C (*Southeast Regional Climate* Center, 2008). Elevation ranges from 350 to 1900 m. Forests are dominated by northern hardwoods (i.e. *Aesculus flava*, *Betula alleghaniensis*, and *Fagus grandifolia*) at higher elevations, mixed hardwoods (*Quercus prinus*, *Q. alba*, and *Oxydendrum arboreum*) on less fertile lower elevation sites, and mixed mesophytic forests (comprised of *Acer saccharum*, *Q. rubra*, and *Carya* spp. among others) on lower slopes and in coves (SAMAB, 1996). Soils consist of Utisols on gradual slopes and ridges, and Inseptisols on steeper slopes and coves (Graham, 1990). The biological diversity of herbaceous communities is particularly rich, especially in mesic cove forests (Ford et al., 2000; Glenn-Lewin, 1977).

This region of the Southern Appalachians has a history of extensive timber harvesting in the 1800s and early 1900s, followed by land abandonment and natural reforestation that began in the mid-1900s and has continued to the present (Eller, 1982; Gragson and Bolstad, 2006). Although today much of the land is forested, timber harvesting continues throughout the region, resulting in a patchwork of forest stands in different successional stages. Prior

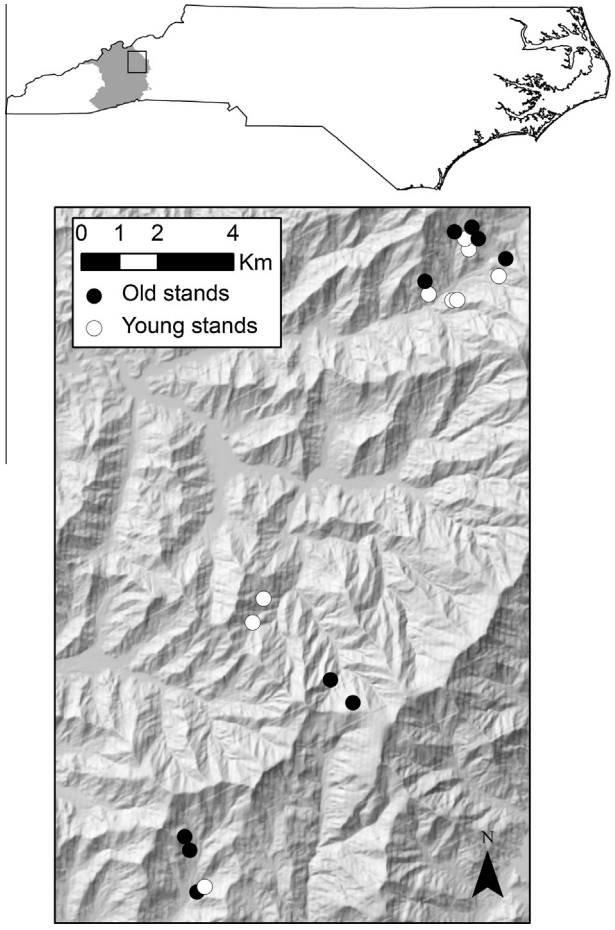

Fig. 1. Map of the French Broad River watershed (shaded area, top panel), western North Carolina, and the 19 study plots (20 × 20 m) showing topography using the Hillshade feature in ArcMap (bottom panel).

to the 1960s, timber harvesting often involved taking the large valuable trees and leaving behind the smaller trees of less marketable species, with no efforts made to minimize soil disturbance or erosion. In the 1960s–1990s, the US Forest Service replaced selective cutting with clear-cutting, usually in large blocks containing smaller cuts of 10–12 ha bordered by narrow strips of uncut forest and logging roads (Petranka et al., 1993).

2.2. Study species

P. lanuginosa (Family Liliaceae; yellow fairybells, formerly *Disporum lanuginosum*) is a perennial herb characteristic of moist wooded slopes and coves (Radford et al., 1968). It is distributed throughout the Appalachian mountains of eastern North America, ranging from the Southern Appalachian chain as far south as Alabama northward through Ontario. *P. lanuginosa* was found to be more abundant in old (>85 years) than in 25–50 year old logged forest stands in Georgia (Ford et al., 2000), and also had lower mean coverage in recently logged stands than older stands in the study region in 1996 (S. Pearson, unpublished data). *P. lanuginosa* blooms in early spring, often with two pale yellow flowers terminating on each of 1–8 branching stems. Fruits are orange to red ellipsoid berries, containing one to five seeds per fruits. Little is known about the pollination of *P. lanuginosa*, but field observations suggest that bumblebees are important pollinators (personal obs. M. Jackson). The genus *Prosartes* is non-clonal and does not undergo vegetative spread (Lezberg and Antos, 1999).

2.3. Field methods

We identified 19 populations of *P. lanuginosa* occurring in "old" and "young" forest stands, all within three watersheds in the Craggy Mountain range of western North Carolina (Fig. 1). Stand age was estimated from US Forest Service CISC (Continuous Inventory of Stand Condition) data followed by visual inspection of stands in the field. We classified "old" stands as those that were harvested by selective logging prior to 1920 and not cut since then ($n = 10$). "Young" stands were clear-cut between 1970 and 1990 and have since naturally re-established ($n = 9$). Thus, all stands were historically logged; we compared stands logged >∼90 years ago to stands logged ∼20–40 years ago. Populations were located by first generating random points within US Forest Service CISC stand age classes using ArcMap and then searching for the closest patch of *P. lanuginosa* individuals. We established permanently marked 1 × 2-m quadrats ($n = 1$–8 per plot) around groups of individuals, all within a 20 × 20-m plot that encompassed a subset of the larger population. Within the quadrats, the location of each *P. lanuginosa* plant was mapped to the nearest centimeter. At least 20 individuals were mapped in each plot; once a quadrat was established, all plants of the focal species within the quadrat, including new recruits, were monitored.

We measured morphological characteristics related to aboveground biomass for every *P. lanuginosa* individual within the quadrats, including stem height, leaf length and width, and number of flowers and fruits. Measurements were taken during mid-June (peak biomass for most herbaceous species in the region). We measured and monitored the fates of all individuals along with any new recruits for three consecutive years (2009–2011). Populations were sampled in the same order each year, with efforts made to alternate between sampling populations in old and young stands in order to minimize the possibility of temporal bias among sites.

To estimate total aboveground biomass, we derived regression equations to estimate stem biomass, leaf biomass and leaf area by destructively sampling 20–30 individuals (mean adjusted $r^2 = 0.85$; Supplement 1) collected from locations within the region but outside the study plots. Individual leaves and stems were measured in the field, and weighed after oven drying at 65 °C to a constant mass (approx. 24 h). We performed digital image analysis to determine the area of fresh leaves that were scanned within 2 h of collection (O'Neal et al., 2002) using the software ImageJ (Schneider et al., 2012).

To assess environmental differences among old and young stands, a variety of measurements were recorded at the plot- and quadrat-level. These included total herb and shrub cover (%), litter depth, soil characteristics (texture, bulk density, total *N*, organic matter, P, K^+, Ca^{++}, Mg^{++}, and pH) to a depth of 15 cm, canopy closure (average of 5 spherical densiometer readings per plot), aspect, slope, terrain shape, and elevation (using 30-m digital elevation models in ArcGIS). A detailed description of the field sampling procedures is provided in Supplement 2.

Lastly, we conducted a seed-sowing experiment to examine whether germination success and seedling survival of *P. lanuginosa* differed among old versus young stands. In late-summer 2009, we collected seeds from fruiting individuals outside the study plots and sowed 20 seeds within nine 0.5 × 0.5-m microplots (180 seeds/plot). The microplots were evenly spaced within twenty 20 × 20-m plots located within 50 m of the main plant-performance plots. Five of the germination plots had no paired performance plots; these were chosen to represent sites that did not previously contain *P. lanuginosa* populations in order to test for dispersal limitation. In 2010, the experiment was repeated in a subset of four plots to check for a year effect on germination rates.

2.4. Life-stage classification and estimation of demographic parameters

We used the regression equations to estimate total aboveground (stem + leaf) biomass and leaf area (Supplement 1) for each *P. lanuginosa* individual. Relative measures of change (growth) for each time interval between years (2009–2010 and 2010–2011) were obtained by subtracting the values of biomass and leaf area for the proceeding year from the prior year and dividing that difference by the value from the prior year (i.e., [2010 value – 2009 value]/2009 value).

Each *P. lanuginosa* individual was classified into one of five stage classes: seedling, vegetative, small flowering adult, large flowering adult, and dormant. In the concurrent seed-sowing experiment, we found that first-year seedlings ($n = 1652$) had a mean leaf area of 9 cm^2. Therefore, we considered a seedling to be any individual with leaf area <9 cm^2. We recognize that this approach may slightly over- or underestimate the total number of seedlings; however, we chose to use a leaf area threshold rather than first-year status, since we did not know which individuals were first-year plants in 2009 (the first year of the study). Vegetative plants consisted of all non-seedling, non-flowering individuals. Small flowering plants were all flowering individuals with total aboveground biomass less than the median for flowering plants, and large flowering plants had total above-ground biomass equal to or greater than the median. To allow for valid comparisons across populations of the same species and to avoid differences in the categorization of each population (Enright et al., 1995), we chose to subdivide reproductive plants into two categories reflecting apparent threshold size values rather than using Moloney's (1986) algorithm. Sample sizes within each life stage for each stand-age/year combination were large enough (at least 10 individuals) to allow adequate estimates of transition probabilities between categories. Subdividing plants into more stage classes would lead to problems with parameter estimation and low sample sizes within each category. However, assigning plants to one of two flowering stage classes was necessary to account for differential resource allocation between large and small adults.

Dormant plants were individuals from 2009 that did not reappear in 2010 but then reappeared in 2011. We assumed that individuals did not remain dormant for more than one year, thus the dormant-dormant transition probability was set to zero. This may be overly conservative; for instance, Farrington et al. (2009) found a dormant-dormant transition probability of 0.124 for *Panax qunquefolius* (a species with a similar life history) after 8 years of monitoring populations. However, the time frame of this study was too short to accurately estimate multi-year dormancy.

Across annual transitions, plants can grow into larger size classes (growth), remain in the same size class (stasis), regress into small size classes (regression), become dormant (dormancy), return from dormancy (emergence), or die. The one exception to this rule is that all surviving seedlings were reclassified as vegetative plants the following year, since our definition of "seedling" was a first-year plant that emerged from a seed. We obtained transition probabilities by calculating the proportion of individuals in each category experiencing each particular fate from one year to the next. We used the "anonymous reproduction method" (Caswell, 2001) to estimate stage-specific fecundity. First, we estimated the proportional contribution of each adult category to the total reproductive effort, measured as total number of fruits. The total number of seedlings in year $t + 1$ was then allocated to the two flowering adult categories according to their reproductive effort. Lastly, the number of seedlings was divided by the total number of individuals in year t within each adult category to obtain the mean fecundity per category.

2.5. Statistical analyses

Using estimates of transition probabilities and fecundity rates, we constructed a set of summary 5×5 stage-structured Lefkovich population projection matrices (Lefkovitch, 1965) for old stands and young stands for each of two annual transitions (2009–2010 and 2010–2011). The matrices were of the form

$$n_{t+1} = An_t \quad (1)$$

where n_t is a vector of k stage classes and A is a square matrix of dimension k (Caswell, 2001). The elements of A (i.e., a_{ij}) represent transition probabilities between different stages or stage-specific fertilities. The summary matrices were constructed using transition probabilities and fertilities from data pooled across all plots within each stand age category. Pooled data provide a better way of synthesizing the demography of multiple populations than using the average of multiple projection matrices because it accounts for the disproportionate weight that low plant numbers in some size classes and locations can give to transition probabilities (Bruna and Oli, 2005; Horvitz and Schemske, 1995).

Population growth rates and 95% confidence intervals were estimated by first developing bootstrap datasets ($n = 250$) by sampling, with replacement, quadrats from the original dataset. The number of quadrats in the bootstrap dataset was equal to the number of quadrats in the original dataset ($n = 83$). Each dataset was used to estimate the 20 non-zero parameters for the Lefkovich matrix. Values of these parameters were adjusted to remove any bias due to the bootstrap procedure (McPeek and Kalisz, 1993). We used these sample matrices to calculate the relative population growth rate, λ, which was the dominant eigenvalue of each matrix, for old and young stands across the two annual transitions. Values of λ between stand age categories and across years were considered significantly different if their 95% confidence intervals were non-overlapping. We also conducted elasticity analysis to examine the relative importance of each transition probability on population growth (De Kroon and Van Groenendael, 2000). Finally, we calculated the stable-stage distribution (SSD) for each bootstrap matrix, and compared the SSD and the observed distribution in each habitat type and each year using G tests (Caswell, 2001). The SSD, which is the right eigenvector of the transition matrix, was scaled to 100 so that each element of the vector represents the percentage of the population in that stage class (Caswell, 2001).

To quantify the contribution of each transition probability, or groups of transition probabilities, to observed differences in λ between old and young forests and across years, we used a fixed-design Life Table Response Experiment (Caswell, 2001; LTRE; Horvitz and Schemske, 1995). In this type of analysis, a life table appears as the response variable in an experimental design, and "treatments" are then applied to change the vital rates in the life table. In this case, we first used the life table matrices for old forests as the "control" matrices while the matrices for young forests were the "treatment." In a second set of analyses to examine differences in λ across years, we used the 2009–2010 matrices as the "control" and the 2010–2011 matrices as the "treatment." The differences in λ, or $\Delta\lambda$, between control and treatment matrices are given by

$$\Delta\lambda = \lambda^t - \lambda^c \approx \sum (a_{ij}^t - a_{ij}^c) \times (\delta\lambda/\delta a_{ij})\downarrow_{(Ai+Ac)/2} \quad (2)$$

where $(a_{ij}^t - a_{ij}^c)$ is the difference in a_{ij} between the treatment and control matrices, and $\delta\lambda/\delta a_{ij}$ is the sensitivity of λ to changes in a_{ij} evaluated at the mean value (i.e. the matrix "midway" between the two matrices being compared (Caswell, 2001; Horvitz and Schemske, 1995). If the sensitivities of a_{ij} terms in the mean matrices are positive, a negative contribution of a transition probability (or group of transition probabilities) to $\Delta\lambda$ indicates the value of that variable in the treatment matrix is lower than in the control

matrix (and vice versa). Thus, we conducted four LTRE comparisons: one for each combination of stand age (old/young) and annual transition (2009–2010/2010–2011) to decompose the effects of matrix elements on $\Delta\lambda$ across both stand age categories and years. Then, we compared the contributions of transition probabilities to $\Delta\lambda$. The LTRE analyses were conducted using the 'popbio' package (version 2.4) in R (R Development Core Team, 2011; Stubben and Milligan, 2007). It should be noted that we are attempting here to discern the demographic parameters that underlie differences in projected population growth rates between old and young stands that have already occurred, rather than attempting to predict future population dynamics of *P. lanuginosa* in these forest stands. Thus, we are using a retrospective analysis rather than a prospective analysis, which would address the effects of potential future changes and assume that demographic rates remained constant over time (Caswell, 2001; Horvitz et al., 1997).

We used ANCOVA to test for differences in germination and seedling survival (both arc-sin square-root transformed) between old and young stands, with plot included as a random effect. Differences in environmental variables across stands were analyzed using Welch two-sample *t*-tests, and we assessed differences among densities and proportions of *P. lanuginosa* stage classes between old and young forests for each year using *G* tests. We considered differences to be statistically significant if $p < 0.1$ due to small sample sizes.

3. Results

3.1. Plot and year characteristics

Plots represented a range of elevations (887–1509 m), topography, and soils (Supplement 3-4). Plots in old stands had higher total herb cover (48.3% vs. 36.9%, $t = 1.84$, $df = 17.7$, $p = 0.08$), deeper leaf litter (2.0 vs. 1.6-cm, $t = 1.98$, $df = 15.4$, $p = 0.07$), more convex terrain shape indices (22.7 vs. −11.2, $t = 3.16$, $df = 16.5$, $p = 0.006$), greater within-plot variability (standard deviation) in canopy openness (1.89 vs. 1.33, $t = 1.86$, $df = 9.8$, $p = 0.09$), and lower tree density (396 vs. 637 trees/ha, $t = -2.68$, $df = 14.3$, $p = 0.02$). None of the soil variables differed significantly between old and young stands. In old stands, the overstory was dominated by *Quercus rubra*, *Acer saccharum*, and *Carya* spp. (in order of relative basal area), whereas young stands were dominated by *Liriodendron tulipifera*, *Prunus pennsylvatica*, and *Quercus rubra* (Supplement 5).

Precipitation for the spring months of April–June was below average during the second year of the study (2010) compared to 1981–2010 normals (18.5-cm total, −33% normal), but was wetter than average in both 2009 (38.9-cm total, +41% normal) and 2011 (39.5-cm total, +42% normal).

3.2. Germination and seedling survival

The mean germination rate from the seed-sowing experiment for 2009–2010 was 45% (±3.1%) and ranged from 23–68% ($N = 20$ plots; Table 1). These rates did not differ substantially the following year, with a mean germination for 2010–2011 of 50% (±9.4%), with range 26–68% ($N = 4$ plots). Mean seedling survival to the next year was 68% (±3.5%) with range 24–91%. Neither germination rate nor seedling survival differed between old and young stands (Table 1).

Table 1
Mean rates for *P. lanuginosa* germination and seedling survival to the next year for old and young stands, along with 1 standard deviation (in parentheses) and results from a one-way ANCOVA to test for differences in germination and seedling survival across stand age, with plot included as a random effect. $N = 180$ micro-plots nested within 20 plots.

	Old	Young	Combined	*F*	*p*
Germination (%)	43.0 (24.1)	47.9 (20.3)	45.0 (3.1)	0.75	0.397
Seedling survival (%)	68.2 (34.7)	67.1 (25.5)	68.0 (3.5)	0.17	0.689

Table 2
Projected population growth rates (λ) and 95% bootstrap confidence intervals (in parentheses) for *P. lanuginosa* populations in old and young forests across two annual transitions (2009–2010 and 2010–2011).

Year	λ_{Old}	λ_{Young}
2009–2010	0.839 (0.795–0.959)	0.736 (0.693–0.853)
2010–2011	0.783 (0.718–0.943)	0.680 (0.640–0.803)

3.3. Projected rates of population growth and demographic contributions to differences in λ

We monitored a total of 859 *P. lanuginosa* plants (including new recruits) over the three-year study period within the main plant-performance plots, resulting in four sets of transition probabilities and fecundity rates (old and young forests in 2009–2010 and 2010–2011; Fig. 2). Total numbers of *P. lanuginosa* individuals were highest in 2011, followed by 2010 and 2009 (563, 477, and 387 respectively; Supplement 6). Neither densities, above-ground biomass, nor leaf area of stage classes differed significantly between old and young forests across years.

The projected rates of population growth (λ) varied from 0.68 to 0.84 (Table 2). Although overlapping 95% confidence intervals indicated no significant differences among population growth rates, populations in old forests had higher values of λ than young forests across both years, with the upper limits of the CI's approaching, but not crossing, 1. Population growth rates were higher in 2009–2010 (following a wet spring) than in 2010–2011 (following a dry spring) for both old and young forests.

Elasticity values (Supplement 7) provide a measure of relative sensitivity of population dynamics to particular parameters in the Lefkovitch matrix. In all four stand-age/year categories, the largest elasticity values were in stasis transitions (i.e., no change in life stage), including vegetative-to-vegetative for all stand/year combinations (these were highest in young forests) and large flowering-to-large flowering for all stand-age categories in 2009–2010. When summed across regions in the matrix (Fig. 3), elasticities for stasis had the most impact on λ. This is likely because the transition probabilities for stasis were consistently high (Fig. 2) due to the long-lived, slow-growing life history strategy for *P. lanuginosa*. During 2010–2011, fecundity and growth had substantially more impact on λ in old forests (fecundity = 0.11, growth = 0.28) than young forests (fecundity = 0.03, growth = 0.14), whereas stasis had more impact on λ in young forests (0.58) than old forests (0.31; Fig. 3).

In deconstructing differences in λ between old and young forests and across years into contributions from individual transition probabilities, the LTRE comparing old and young stands showed that, across both annual transitions, the lower λ in young forests compared to old forests was due to lower fecundity, growth, emergence, and dormancy and higher regression and stasis in young forests (Fig. 4). Reduced growth (primarily growth from vegetative to flowering) contributed more to reduced λ in young forests during 2009–2010 (which was the drier spring), whereas in 2010–2011 reduced fecundity had a higher contribution. The LTRE comparing years showed that the higher λ in 2010–2011 (the wet spring) was due to primarily to increased stasis of vegetative and large flowering adults and lower fecundity in old forests (Fig. 5). In young forests, the increase in λ in 2010–2011 was due primarily to increased stasis of vegetative and large flowering plants, reduced growth

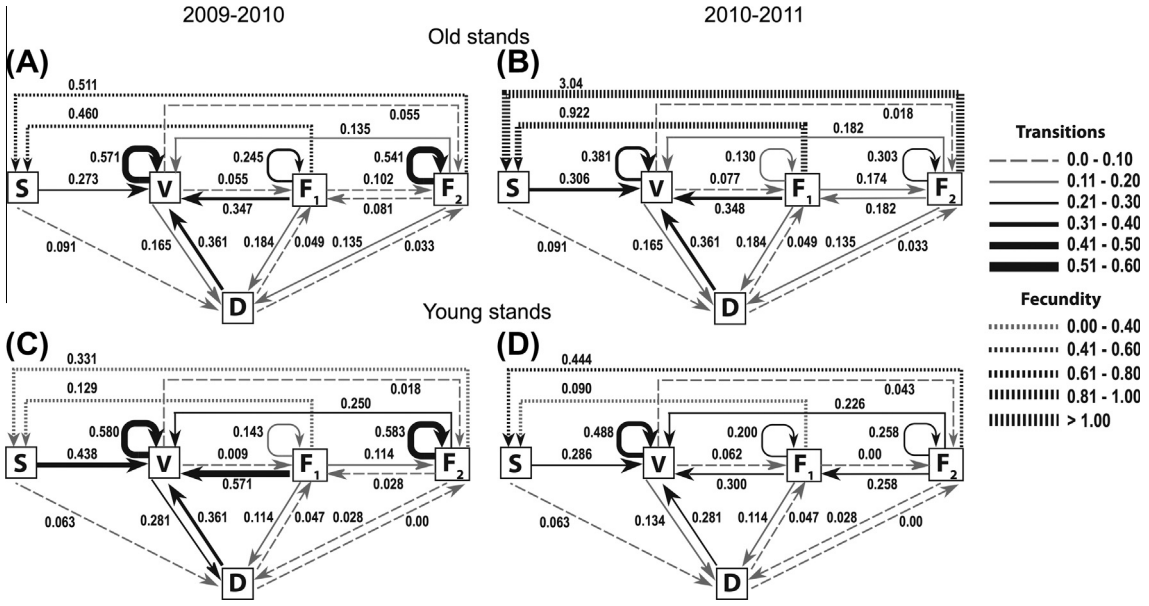

Fig. 2. Life-cycle graphs for *Prosartes lanuginosa* in old forests, 2009–2010 (A) and 2010–2011 (B), and young forests, 2009–2010 (C) and 2010–2011 (D). Arrows indicate potential transitions between four stage classes: seedlings (S), vegetative (V), small flowering adults (F_1), large flowering adults (F_2), and dormant individuals (D). The stage-to-stage transition probabilities and measures of fecundity per individual for each flowering adult life stage (F_1–S and F_2–S) are shown for each stand age-year combination.

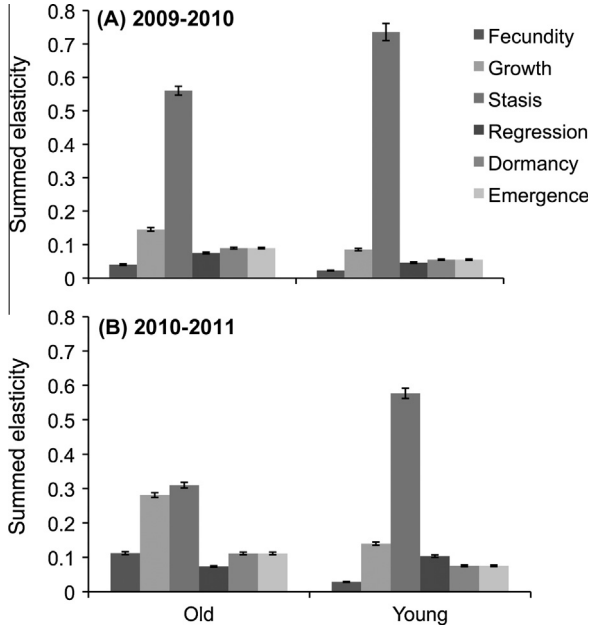

Fig. 3. Summed elasticities of *Prosartes lanuginosa* population growth rate (λ) for life stage categories fecundity, growth, stasis, regression, dormancy, and emergence in old (logged > 90 years ago) and young (logged 30–40 years ago) forest stands. Error bars represent 1 standard error.

from vegetative to flowering life stages, and increase regression from small flowering adults to vegetative.

3.4. Life stage distributions

The stable-stage distribution was significantly different from the observed distribution across both stand-age categories in 2009–2010 (Old: $G^2 = 13.98$, $p = 0.007$, Young: $G^2 = 16.95$, $p = 0.002$) and less so, but still significant with $\alpha = 0.1$, in 2010–2011 (Old: $G^2 = 9.18$, $p = 0.06$, Young: $G^2 = 9.50$, $p = 0.05$; Fig. 6). Dormant individuals were overrepresented (in the observed distribution) in all cases, and seedlings were underrepresented in old forests but not in young forests. The SSD predicted greater proportions of seedlings in old forests. In 2009–2010, vegetative plants were underrepresented and flowering adults were overrepresented, whereas in 2010–2011, vegetative plants were closer to the stable stage distribution, while small flowering plants were underrepresented and large flowering plants were overrepresented.

4. Discussion

This study provided new insights on the effects of timber harvesting on population dynamics of an understory herb species in eastern North American deciduous forests, along with the demographic parameters responsible for reduced plant performance in previously logged stands. Many studies have found long-lasting responses to logging in herbaceous community composition and structure (Duffy and Meier, 1992; Wyatt and Silman, 2010). Such studies are useful "snapshots" of distribution and abundance following disturbance, and can provide integrated, if indirect, views of long-term trends in population dynamics. However, fewer studies have specifically examined plant performance and demography in sites with logging history. Because populations of long-lived perennials can take a long time to respond to changing environmental conditions, estimates of plant performance and population dynamics can provide more informative insight into the long-term trajectories of populations than measures of distribution and abundance alone. Our results showed that disturbances, such as logging, can negatively affect population growth rates for *P. lanuginosa* via reductions in growth from vegetative to flowering life stages and in fecundity.

4.1. Effects of logging history on population growth

As hypothesized, lower population growth rates in young forests across both annual transitions indicate these populations may be at elevated risk of population decline, while populations in old forests may be somewhat buffered from such risk. Results from the LTREs showed that the reduced population growth rates

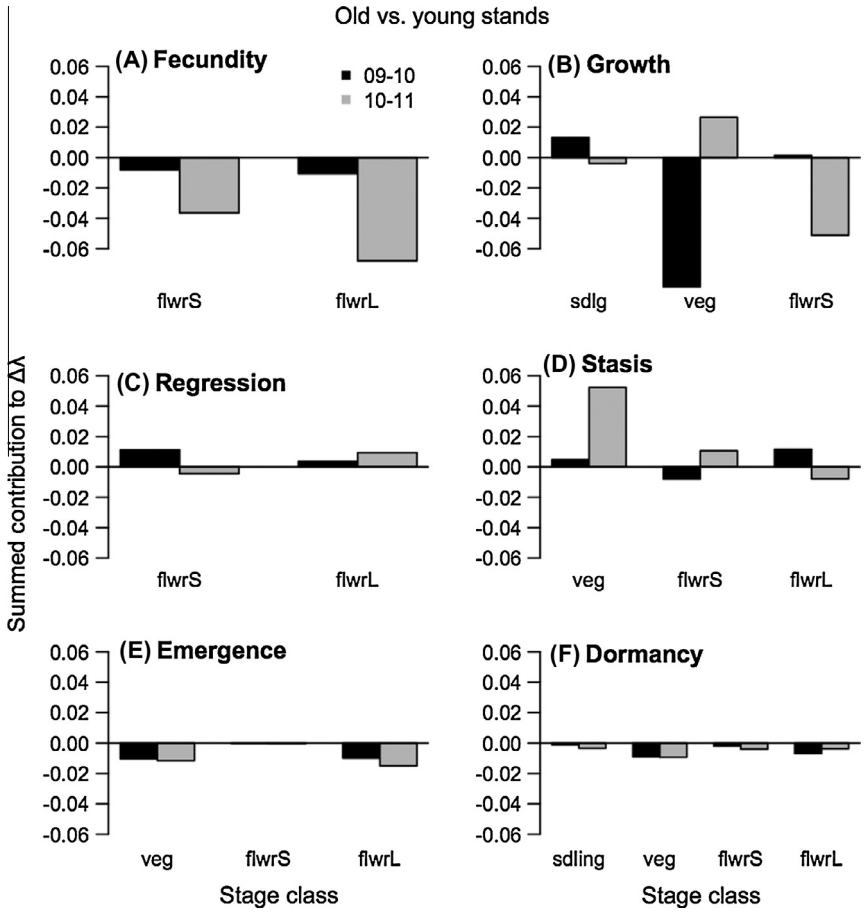

Fig. 4. Life table response experiment (LTRE) summed contributions to differences in population growth rate ($\Delta\lambda$) of matrix elements representing fecundity, growth, regression, stasis, emergence and dormancy. Comparisons are between old and young forests; thus, a negative contribution from a matrix element implies that lower values for that transition contributed to the smaller λ in young stands compared to old. A separate LTRE was conducted for each annual transition (2009–2010 and 2010–2011). Stage classes are seedling (sdlg), vegetative (veg), small flowering adults (flwrS) and large flowering adults (flwrL).

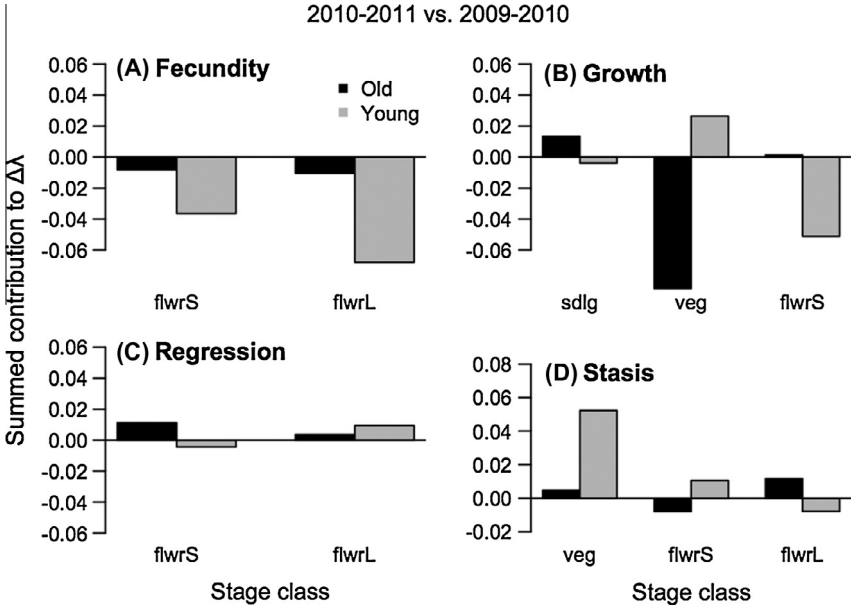

Fig. 5. Life table response experiment (LTRE) summed contributions to differences in population growth rate ($\Delta\lambda$) of matrix elements representing fecundity, growth, regression, and stasis. Comparisons are between the two annual transitions of the study period; thus, a negative contribution from a matrix element implies that lower values for that transition contributed to the smaller λ in 2010–2011 compared to 2009–2010. A separate LTRE was conducted for each stand age category (old vs. young). Emergence and dormancy contributions are not shown because the transition probabilities related to emergence and dormancy were set equal across years, so their contribution to $\Delta\lambda$ was zero. Stage classes are seedling (sdlg), vegetative (veg), small flowering adults (flwrS) and large flowering adults (flwrL).

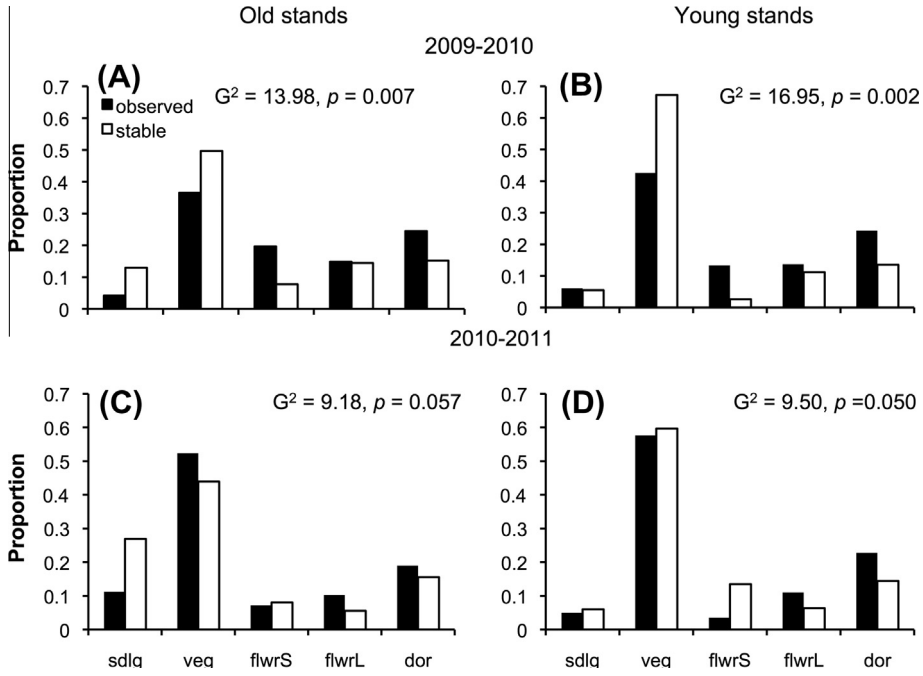

Fig. 6. Observed proportion of *P. lanuginosa* individuals in each stage class (sdlg = seedling, veg = vegetative, flwrS = small flowering adult, flwrL = large flowering adult, dor = dormant) compared to the projected stable stage distribution across both annual transitions (A–B: 2009–2010, C–D: 2010–2011) in old forests (logged > 90 years ago) and young forests (logged 20–40 years ago). The 2009–2010 annual transition contained a drier than average spring, and 2010–2011 contained a wetter than average spring. G^2 statistic and corresponding *p*-value indicate the results of *G* tests comparing SSDs and observed distributions in each habitat type and year.

in young forests were largely attributable to reduced growth from vegetative to flowering stages (2009–2010) and lower fecundity of large and small flowering plants (2010–2011). These results were also reflected in the elasticity values, which showed that fecundity and growth had substantially more impact on λ in old versus young stands. The 2009–2010 annual transition included a very dry spring, suggesting that drought may exacerbate population decline in young forests via reduced growth to adult life stages. Reduced fecundity in young forests in 2010–2011 likely resulted from the reduction in growth following the previous year's drought, perpetuating a cycle of population decline. These results agree partially with those of Jacquemyn and Brys (2008), who found higher population growth in older forests for a temperate forest herb, *Primula elatior*, due to increased seedling and juvenile growth and increased juvenile and adult survival. However, they found higher rates of adult growth in young forests relative to old forests, indicating that once established, plants grew better in young forests. Our results conversely suggest that for *P. lanuginosa*, population growth is limited by logging history at multiple life stages including fecundity, not just seedling establishment.

Although we did not attempt to disentangle the direct environmental drivers of *P. lanuginosa* population declines following logging, it is likely that changes in forest composition and structure that develop following logging partially explain differences in plant performance between old and young stands (see Meier et al., 1995 for a comprehensive discussion of mechanisms for loss of herb diversity following logging). For example, we found greater standard deviation of canopy closure in old stands, possibly indicating the presence of more canopy gaps. Meier et al. (1995) found that *Cimicifuga americana*, a similar long-lived perennial typical of the study region, relies on canopy gaps for fruiting, and *Primula vulgaris* showed higher population growth rates under canopy gaps in Europe (Valverde and Silvertown, 1998). Related to this, microtopography created by fallen trees that is typical in old forests can enhance germination and growth of forest herbs (Bratton, 1976; Flinn, 2007a). Such microtopography is lost in recently clear-cut stands. Thus it is possible that forest herbs such as *P. lanuginosa* are capable of withstanding severe forest disturbance but decline in later years as dense sapling stands develop. This interpretation is consistent with Ford et al. (2000), who found that in very young stands (15 years), *P. lanuginosa* was still present (implying it was not extirpated by logging) but less abundant than in >85 year-old stands, and absent in older clear-cut stands (20–50 years old).

4.2. Inter-annual differences in population growth

Following a drier than average spring in 2010, population growth rates were lower in 2010–2011 across all stands. However, the demographic mechanisms behind these declines were different in old versus young stands. In old forests, lower population growth rates in 2010–2011 were driven primarily by reduced fecundity, while in young forests, reduced growth from vegetative to flowering and increased regression from small flowering to vegetative stages were more important. Because populations of flowering adults are more established in old forests, overall population growth rates may be more sensitive to fecundity parameters, whereas in young forests, growth from vegetative to flowering life stages is more important in determining year-to-year population trajectories. For example, small flowering plants in young forests likely have fewer energy reserves than large flowering plants and are thus more likely to regress back to a vegetative state in years with harsh conditions (i.e., drought; Abrahamson and Caswell, 1982), while in old forests, small flowering adults might be less energy-limited (and can perform equally to large flowering adults).

This analysis emphasizes differences in demography among years and with respect to forest stand age. In our analyses, all populations of *P. lanuginosa* had growth rates that were significantly <1 in both years, which suggests that these populations are declining. However, this result is partially due to our assumption that all plants remaining dormant for more than 1 year were dead. This assumption overestimates mortality, but we did not have sufficient data to estimate rates of survival while dormant, and studies have

found that plants that exhibit dormancy rarely do so for >1 year (Lesica, 1994; but see Shefferson, 2009). Therefore, we made the conservative choice to set these rates to 0. Our projections represent a snapshot of these populations in time, and values of λ measure relative population growth rates assuming demographic rates and environmental conditions remain constant (Caswell, 2001). Thus, we do not attempt to predict the future population dynamics of *P. lanuginosa* in these sites; rather, we focus on discerning the demographic factors underlying differences in λ across stand-age categories and across years.

4.3. Beyond establishment vs. dispersal limitation

Many studies have attempted to discern whether the recolonization of plant species in sites with historic land use is hindered by dispersal (seed availability) or establishment limitation (Clark et al., 2007; which only involves survival beyond the seedling stage; see Turnbull et al., 2000). Our study takes this debate a step further, focusing on the performance (survival, growth, reproduction) of plants following establishment. While we do investigate dispersal and establishment limitation, our data show important differences beyond the seedling stage in the growth and fecundity of post-seedling plants. In the seed-sowing experiment, seedling survival (i.e. the seedling-vegetative transition) was high and did not differ between old and young stands. Even in the natural populations, growth from seedling to vegetative actually contributed positively to population growth in young forests. Therefore it appears, given an adequate seed supply, seedling establishment does not hinder population growth in young forests (that were logged 20–40 years ago); rather, processes occurring in later life stages (i.e., the vegetative to flowering transition and fecundity) are more important.

Our finding no difference in experimental germination success between old and young forests following seed-sowing indicates that dispersal limitation may also play a role in hindering recolonization for *P. lanuginosa* as hypothesized. In addition to limiting recolonization of unoccupied forest stands, dispersal limitation can be important at fine scales (Pearson and Fraterrigo, 2011). Even if populations remain extant at the scale of a forest stand, disturbances may increase the patchiness of herbaceous populations within a forest stand due to increased mortality rates or changes to soil conditions (Fraterrigo et al., 2006; Goodale, 2001). After the disturbance, dispersal limitation can extend the time required to restore individuals to unoccupied microsites within the stand.

Despite the lack of a stand-age effect in the germination experiment, the LTRE indicated that, at least in 2010–2011, natural germination was lower in young forests (because germination is incorporated into measures of fecundity). Therefore, it could be that processes occurring between fruiting and germination (i.e., dispersal into suitable microsites within a stand) are hindered in young forests. In the seed-sowing experiment, seeds were sown to maximize germination potential (i.e., placed under a small amount of soil with removal of all vegetation within 0.5×0.5-m), so these processes may have been masked. If the number of flowering adults is reduced in young forests, lower fruit production along with low rates of germination will combine to lower overall recruitment.

It is worth noting that all of the old stands used in this study were logged, some as recently as 90 years prior to the study. Wyatt and Silman (2010) argue that mature secondary forest stands are too young to serve as baselines for recovery. They found that species richness and individual abundance was greater in old growth (never logged) stands than in 100–150 year-old forests. Therefore it is likely that our old stands are still in a state of recovery and may take centuries to reach the successional state of old growth forests, if they do at all. This is supported by our finding that the stage structure of *P. lanuginosa* populations differed significantly from the stable stage distribution in both old and young forests, which countered our original hypothesis that the stage structure of populations in old stands would be closer to stable. Jacquemyn and Brys (2008) found that populations of *Primula elatior* reached population growth rates of $\lambda > 1$ only once a threshold forest age of 150 years had been exceeded. Even some of our "old" forest stands were <150 years old. If the study populations of *P. lanuginosa* are declining at the rates predicted by λ, they would not survive long enough to reach this threshold forest age. We believe the more likely scenario, though, is that population growth rates will continue to vary among years, and in the absence of further disturbance, populations will gradually recover to pre-disturbance states.

Climate warming (projected to range from 1–7 °C in the region Mearns et al., 2003), including more frequent drought years, is expected to interact with land-use legacies in ways that are difficult to predict (Thuiller et al., 2008). Although we lack sufficient data to explicitly test for links between climate and population dynamics, our results lead us to believe that *P. lanuginosa* populations in recently logged stands may fare worse than their old-stand counterparts under climate change. The demographic responses to a drought year differed in old versus young stands, with populations in young forests showing reduced growth from vegetative to flowering stages and populations in old forests lowering fecundity. Under warming and drying conditions, these results suggest that populations in young forests, although able to persist through vegetative stasis, may not produce enough mature flowering adults to perpetuate the populations. Thus, climate warming may interact with land-use history in these sites to perpetuate population decline.

5. Conclusions

We show that the long-term recovery of *P. lanuginosa* populations in young forests may be compromised. Populations in young forests showed lower recruitment from vegetative to flowering life stages and reduced fecundity. In a drought year, these populations responded by remaining vegetative (not transitioning to a flowering stage) and by regressing from small flowering to vegetative, similarly to the findings of Endels et al. (2004) who found low proportions of flowering adults of three forest herbs in young forests compared to old. Our results indicate that the effects of recent logging on a forest understory herb species are likely determined by differences in adult plant performance (as opposed to seedling establishment), combined with dispersal limitation, that may persist for decades. This conclusion is in agreement with the findings of Verheyen and Guntenspergen (2003), who suggest the existence of a two-stage colonization process. Seed availability and dispersal determines the initial distribution of the population in the habitat patch. Then, fine-scale environment conditions modulate the growth, survival, and reproduction of those new colonists. Flinn (2007b) also showed that interactions among environmental variables within young stands hindered forest understory plant colonization. These results imply that environmental conditions in young forests hinder performance of a native herb and confirm the usefulness of multiple measures of performance and population dynamics (used, when possible, in combination with distribution and abundance measures) for quantifying current and projected effects of land-use history on forest plants.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2013.05.049.

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