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MICROSITE-LIMITED RECRUITMENT CONTROLS FERN COLONIZATION OF POST-AGRICULTURAL FORESTS

Kathryn M. Flinn[1]

Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, New York 14853 USA

Abstract. Assessing the relative roles of dispersal limitation and environmental effects in population dynamics and community assembly is fundamental to understanding patterns of species distribution and diversity. In forests growing on abandoned agricultural lands, both legacies of vegetation disturbance and changes in the abiotic environment shape the diversity and composition of recovering communities. Here I specify how interactions among historical, environmental, and biological factors influence species distributions, focusing on three fern species with contrasting distributions across forests of different history in central New York, USA: *Dryopteris carthusiana*, *Dryopteris intermedia*, and *Polystichum acrostichoides*. Using population surveys, spore-trap and spore-bank studies, and a three-year field experiment, I compare demographic rates among species and between forest types to determine which life history stages limit colonization and which traits explain species distributions. Adult plants of all three species were larger and more likely to produce spores in post-agricultural forests than in adjacent, uncleared stands. Though lower population densities led to fewer spores in post-agricultural soils, spore availability still exceeded recruitment by four to five orders of magnitude. Sowing additional spores had relatively little effect, while microhabitat conditions had the greatest impact on establishment rates. Given similar microsites, the two forest types had equal rates of establishment, but some forest-floor features preferentially occupied by juvenile plants were less frequent in post-agricultural stands. The availability of suitable sites for establishment, created by small-scale heterogeneity on forest floors, thus limits both the growth of fern populations and the colonization of new habitats. In fact, reduced microtopographic variation in post-agricultural forests may represent a greater hindrance to plant establishment than changes in mean environmental conditions. Among the three fern species, establishment rates differed as species distributions would predict, with the strongest colonizer consistently having the highest rates and the slowest colonizer the lowest. Rather than random or trait-mediated dispersal, the different distributions of these species reflect life history traits that determine establishment rates and thus colonization ability. This case study demonstrates that ecological interactions based on the unique life histories of individual species can override dispersal in determining species distributions.

Key words: colonization; dispersal; diversity; environmental heterogeneity; establishment; ferns; land-use history; life history; population dynamics; recruitment; restoration; succession.

Introduction

Communities recovering from disturbance present an ideal context for assessing the relative strengths of dispersal limitation and environmental control in community assembly. Disturbances not only remove vegetation from suitable sites, creating unoccupied habitats that plants must colonize from seed banks or outside sources, they also cause changes in the abiotic environment that may favor the establishment of certain species (Pickett and White 1985). The most radical and extensive disturbance of many landscapes across Europe and eastern North America in the past several centuries has been the clearance and abandonment of farmland (Kauppi et al. 2006). Changing land use has created ample opportunity to examine how regional dispersal and the local environment shape community composition as forests regrow and to understand the relative roles of processes underlying distribution and diversity patterns.

Herbaceous plant communities, which represent the majority of plant diversity in temperate forests, consistently show lower species richness in forests on abandoned farmland than in forests that were never cleared for agriculture, even centuries after reforestation (reviewed by Flinn and Vellend 2005). Two main classes of mechanisms could control the recolonization of post-agricultural communities: either the process of dispersal into the sites or the process of establishment and persistence after arrival may limit population growth and species distributions. Several lines of evidence, including the overrepresentation of strong dispersers in

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[1] Present address: Department of Biology, McGill University, 1205 Docteur Penfield, Montreal, Quebec H3A 1B1 Canada. E-mail: kathryn.flinn@mail.mcgill.ca.

post-agricultural forests, suggest that dispersal limitation plays a dominant role in the recovery of plant diversity (Matlack 1994, Verheyen et al. 2003, Flinn and Vellend 2005). However, few studies have explored the possibility that interactions with the abiotic environment also influence the composition of post-agricultural forests by determining which species establish and persist. Environmental legacies of agriculture, such as changes in soil nutrient availability, may last as long as 2000 years (Dupouey et al. 2002, Flinn and Marks 2007) and either enhance or depress plant performance (Donohue et al. 2000, Vellend 2005). Though many forest herbs have low fecundity and lack adaptations for long-distance dispersal (Whigham 2004), the relative importance of dispersal and establishment limitation may also vary among species with different life histories. Individual species' demographic responses to post-agricultural habitats certainly shape the early stages of old-field succession (Keever 1950); as forests mature, they may continue to influence community composition and could prove crucial to the recovery of species diversity.

One common pattern that dispersal limitation fails to explain is variation in colonization success among species with similar dispersal abilities. For example, several fern species native to the deciduous forests of eastern North America differ in their relative frequency across habitats of different history (Whitney and Foster 1988, Singleton et al. 2001, Bellemare et al. 2002). Ferns and other plants that produce vast quantities of windblown spores have long been thought to have great and effectively equivalent capacities to migrate across landscapes (Tryon 1970). Since ferns also lack many of the biotic interactions with pollinators, seed vectors, and herbivores that affect seed plants, their distributions should more directly reflect abiotic environmental gradients (Barrington 1993). These attributes make fern communities ideal for focusing on the role of environmental conditions in determining species distributions. Several recent studies have used ferns to investigate spatial and environmental correlates of community composition (Tuomisto et al. 2003, Karst et al. 2005), but the mechanistic basis of species distribution patterns remains unknown. In fact, despite the importance of ferns in many community types, we know remarkably little about how fern populations establish, reproduce, and maintain themselves (Werth and Cousens 1990, Sheffield 1996). The species-specific distributions of ferns in post-agricultural forests suggest that detailed comparisons of their population biology could reveal unique habitat interactions, increasing our understanding of dispersal and environmental effects on forest recovery and on community assembly more generally.

This paper presents a case study of how historical, environmental, and biological factors control species distributions. Specifically, it compares the demography of three fern species with contrasting distributions across the post-agricultural landscape of central New York in order to address two main questions. First, which life stages limit the colonization of post-agricultural forests? Second, which species traits explain the variation in colonization success? Among the three fern species and between forests with different histories, I compare the density, size, and fecundity of adult plants; the availability of spores deposited by the wind and stored in the soil; the rates of plant establishment in various microsites; and the distribution of juvenile plants across these microsites.

METHODS

Sites

Tompkins County, a 1250-km^2 area in the Finger Lakes region of central New York state, USA (42°26′ N, 76°30′ W), has a well-documented history of changes in forest cover over the past 200 years. Forests covered virtually all of the county's land area before European settlement in the 1790s (Marks and Gardescu 1992), and clearing for agriculture then reduced forest area to a minimum of 19% in 1900 (Smith et al. 1993). With later farm abandonment, forests regrew to cover 54% of the landscape by 1995 (Flinn et al. 2005). Spatially and temporally explicit reconstructions of land-use change for every forest stand in the county distinguish forests that were never cleared for agriculture (primary forests) from forests that established on former agricultural fields (secondary forests; Smith et al. 1993, Flinn et al. 2005).

I conducted this study in 20 pairs of adjacent primary and secondary forests spread throughout Tompkins County. All sites were located in mesic, upland forests and placed so that the adjacent stands had a similar slope, aspect, elevation, and soil type (for site attributes, see Flinn and Marks 2007: Appendix). Based on aerial photographs and field evidence including the lack of pit-and-mound microtopography, I chose sites where the secondary forests had developed on plowed fields 85–100 years ago (Smith et al. 1993, Marks and Gardescu 2001, Flinn and Marks 2007). Each stand covered at least 1 ha.

To relate plant performance to environmental conditions in each stand, I used two axes from a principal components analysis of soil nutrient data, which represented gradients in pH and organic matter content (OM; for details, see Flinn and Marks 2007). Together these axes explained 65% of the variation in 13 soil properties measured in composite samples of 20 soil cores collected in each stand. As a measure of light availability, I used the mean amount of radiation transmitted to the understory (measured in moles per square meter per day), estimated from 20 canopy photographs taken in each stand (Flinn and Marks 2007). Within sites, I took the soil cores and canopy photographs along the same four transects where I sampled plant density and performance.

Species

This study focuses on the three most common fern species of mesic, upland forests in central New York

(Mohler et al. 2006): *Dryopteris carthusiana* (Villars) H. P. Fuchs, *Dryopteris intermedia* (Muhlenberg ex Willdenow) A. Gray, and *Polystichum acrostichoides* (Michaux) Schott. I chose these species because, despite similar ecology and life history, they have contrasting distributions across forests of different history. In central New York, *D. carthusiana* is more frequent in secondary forests than in primary; *D. intermedia* is equally frequent in the two forest types; and *P. acrostichoides* is among the herbaceous species most strongly associated with primary forests (Singleton et al. 2001). The adult, sporophyte plants of all three species are long-lived perennials, with leaves growing from short rhizomes. In the independent, haploid phase of the life cycle, spores form heart-shaped gametophyte plants <5 mm wide and a single cell thick, which, upon fertilization, yield juvenile sporophytes.

Adult plant performance

To compare the performance of adult plants between forest types, I quantified plant density, size, and fecundity in the 20 pairs of adjacent primary and secondary forests. In each stand, I counted and measured all individuals of the three fern species along four transects perpendicular to the land-use boundary, 20 m apart, 100 m long, and 2 m wide. Where densities were low, I searched the remainder of the hectare until I had measured at least 40 plants or all I could find. Having developed regression equations to estimate leaf area and spore production from simple measurements (Appendix A), I used total leaf area as a measure of plant size and the leaf area bearing sori as a measure of fecundity. I compared population density and individual plant size between paired primary and secondary forests using mixed models with land-use history as the independent variable and site as a random factor (SAS Proc Mixed; SAS Institute, Cary, North Carolina, USA). Similar models, with a binary response and an additional factor to account for total leaf area, evaluated the odds of producing spores for individual plants of a given size in primary and secondary forests (SAS Proc Logistic). Likewise, I used mixed models with a covariate for plant size to evaluate the effects of land-use history on individual fecundity. To assess the relative influences of land-use history and stand-level environmental conditions on population performance, I used mixed models with site as a random factor and history, soil pH, soil OM, and light availability as independent variables. Population-level performance measures included median leaf area, the proportion of plants that produced spores, and among plants producing spores, the median leaf area with sori.

Spore dispersal and the spore bank

To focus on spore dispersal from source populations in primary forests into secondary stands, I chose two sites where *P. acrostichoides* was restricted to the primary forests. At these sites, *D. intermedia* plants were about half as dense in the secondary forests as in the primary forests and *D. carthusiana* was uncommon. I used microscope slides coated with petroleum jelly to trap airborne spores, placing them 1, 2, 3, 5, 10, and 25 m into both stands along three transects perpendicular to the land-use boundary (Peck et al. 1990, Penrod 1994). As the spores of these species begin to mature in late June in central New York (K. Flinn, *personal observation*), I set fresh traps every two weeks from 26 June to 2 October 2001. With a key I developed by examining spores collected directly from reproductive plants, I identified and counted the fern spores on each slide using the Vernier scale of a compound microscope. To quantify the spore bank in primary and secondary forest soils, I counted and identified germinants from soil cores taken from the same locations at which traps were placed. I collected soil cores on both 26 June and 2 October 2001 to reflect spore abundance before and after seasonal deposition (Penrod and McCormick 1996; for more details, see Appendix B).

I used mixed models with site as a random factor and date as a repeated measure to compare spore density in the air and soil of primary and secondary forests. These analyses modeled the covariance among samples from the same location with an autoregressive structure, in which correlations within locations decrease with time between measures (Littell et al. 1998). Using similar models with an additional factor for distance from the land-use boundary, I also tested whether spore density within secondary forests declined with distance from primary forests.

Gametophyte and sporophyte establishment

I conducted a three-year field experiment to compare establishment rates between forest types, among species, and under varying microhabitat conditions. In three pairs of primary and secondary forests, I sowed spores of the three fern species and left control plots unsown on three forest-floor substrates and at ambient and elevated humidity, in a fully factorial design. For this experiment, I again chose sites where adult plants were present in the primary forests, but rare or absent in the secondary forests, so that sowing spores introduced the species into unoccupied habitats. At each site, I located five 1 × 1.5 m blocks at random positions in both stands. Within the blocks, the species, substrate, and humidity treatments were fully crossed and completely randomized in 4 × 6 arrays of 25 × 25 cm plots. The substrates included leaf litter, left undisturbed; humus, with leaf litter removed; and mineral soil, where litter and humus were removed and the soil overturned with a trowel. These represent the most common forest-floor substrates that could be effectively replicated. To simulate moist, protected microhabitats, I maintained elevated humidity by covering plots with transparent plastic containers (for more details, see Appendix B). I imposed the treatments and sowed spores 31 July through 2 August 2002, then followed the resulting gametophyte and sporophyte

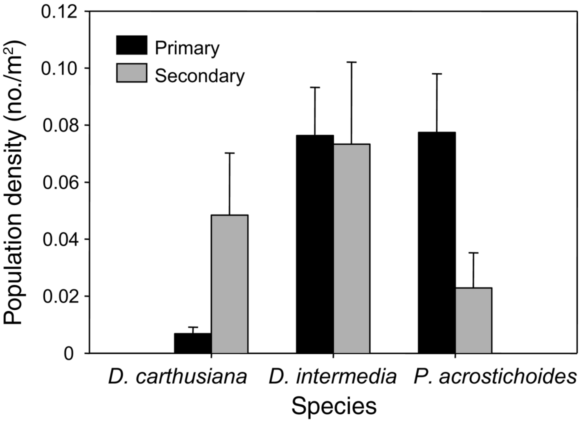

FIG. 1. Population density (mean + SE) of three fern species (*Dryopteris carthusiana*, *Dryopteris intermedia*, and *Polystichum acrostichoides*) in primary and secondary forests of central New York State, USA ($N = 20$ pairs of adjacent primary and secondary forests).

plants through May 2005, sampling the plots monthly from May to November. Since the size and density of gametophytes and sporophytes made marking and following individuals impossible, I quantified the percentage cover of gametophytes in each plot using a 25-cell grid and counted the number of sporophytes.

These variables had distributions with many zeroes, few moderate values, and some extremely high values. For statistical analysis, I treated the presence of gametophytes and sporophytes as binary variables. In addition to the effects of land-use history, humidity, substrate, and spore sowing, fixed factors tested the effects of year, month, and month within year, and random factors accounted for the pairing between stands at each site, the blocks within each stand, and the repeated sampling of each plot. To incorporate random effects and categorical responses, I used generalized linear mixed models (SAS Proc Glimmix; Appendix C). I also evaluated the effects of all treatments on the odds of having surviving sporophytes at the end of the experiment in May 2005. For plots having sporophytes at any time, I tested treatment effects on the number of sporophytes using a model with a Poisson-distributed response and a log link function.

Juvenile plant distribution in relation to microhabitat

To test whether microsite availability could limit colonization, I assessed the distribution of juvenile plants and the frequency of suitable microsites along four 2-m-wide transects through each of the 20 pairs of forests. Sporophytes formed during the present or the previous growing season can be distinguished from older plants and identified to species by their distinctive juvenile leaves, which I recognized by comparison to plants raised from spores. For each juvenile plant, I recorded the substrate it grew on, whether leaf litter, humus, mineral soil, wood, moss, grass, or stone, and whether the substrate was associated with a larger feature, such as a rotten log, a tree root, a treefall pit or mound, or a pool or rivulet of water. I quantified the frequency of these features on forest floors by recording which was present at points at every meter of the four 100-m-long transects in each stand. I compared the proportions of occupied and available substrates with G tests for goodness of fit, and I compared the proportions of primary and secondary forest floors covered by each feature with paired t tests.

RESULTS

Adult plant performance

Across all sites, the mean population density of *Dryopteris carthusiana* was about seven times higher in secondary forests than in primary (Fig. 1), but comparing adjacent stands, population densities did not differ significantly between the two forest types (Table 1). *Dryopteris intermedia* had nearly equal mean population densities across primary and secondary stands, but primary forests had significantly higher population densities than adjacent secondary forests. For *Polystichum acrostichoides*, mean population density was over three times greater in primary forests than in secondary, and population densities were significantly higher in primary forests than in adjacent secondary forests.

By all measures, the performance of adult plants was either comparable or enhanced in secondary forests relative to primary. Plants of all three species were larger and more likely to produce spores in secondary forests than in adjacent primary forests in all but one instance (*D. intermedia*'s odds of reproduction; Table 2). In fact, *D. carthusiana* and *P. acrostichoides* plants of a given size had over 50% higher odds of producing spores in secondary forests than in adjacent primary forests. While *Dryopteris* individuals had similar fecundity in the two forest types, reproductive plants of *P. acrostichoides* with the same total leaf area had one-third more leaf area with sori in secondary forests than in primary.

Accounting for variation in soil nutrients and light availability, populations of all three species had similar median plant sizes in adjacent primary and secondary forests (Table 3). Though the only significant relationship between an environmental variable and plant size was the effect of light in *D. intermedia*, present light and soil conditions had a greater influence on plant size than past land use. However, independent of environmental effects, the proportion of individuals that produced spores was higher in secondary-forest populations of all three species. Forest history had a greater impact than light availability on the reproductive proportion of populations in both *Dryopteris* species, whereas for *P. acrostichoides*, the proportion of reproductive plants depended most strongly on light and soil OM. The median fecundity of *D. carthusiana* populations increased with light levels and did not vary with forest

TABLE 1. Population densities (mean ± SE) of different life stages in primary and secondary forests, for three fern species in central New York, USA.

Life stages	No. individuals/m^2, primary forests	No. individuals/m^2, secondary forests	F	P
Dryopteris carthusiana				
Adult plants	0.0068 ± 0.0023	0.0484 ± 0.0218	3.53	0.0758
Spores produced	14 820 ± 6295	183 500 ± 92 770	0.20	0.6612
Spores deposited	1205 ± 381	918 ± 239	0.46	0.4969
Spores in soil	147 ± 65	108 ± 33	0.31	0.5755
Juvenile plants	0.0003 ± 0.0003	0.0015 ± 0.0010	1.61	0.2201
Dryopteris intermedia				
Adult plants	0.0763 ± 0.0169	0.0733 ± 0.0288	5.38	0.0317
Spores produced	321 600 ± 105 100	306 400 ± 114 900	5.76	0.0266
Spores deposited	13 890 ± 3993	5108 ± 635	7.00	0.0084
Spores in soil	3026 ± 570	2348 ± 489	1.18	0.2793
Juvenile plants	0.0051 ± 0.0022	0.0090 ± 0.0034	0.08	0.7801
Polystichum acrostichoides				
Adult plants	0.0774 ± 0.0206	0.0229 ± 0.0123	19.7	0.0003
Spores produced	81 010 ± 21 060	50 500 ± 24 220	16.5	0.0007
Spores deposited	32 540 ± 6318	8781 ± 1271	22.9	<0.0001
Spores in soil	2810 ± 487	1867 ± 352	2.79	0.0972
Juvenile plants	0.0023 ± 0.0022	0.0001 ± 0.0001	1.30	0.2678

Notes: Mixed models with site as a random factor compare population densities between adjacent primary and secondary forests. Adult and juvenile plant density and spore production were natural-log-transformed after adding one individual. Comparisons of spore deposition and the spore bank included an additional factor to account for repeated samples over the season. Adult and juvenile plant density and spore production estimates represent surveys of 20 primary–secondary forest pairs. Spore deposition and spore bank estimates represent 503 slide trap samples and 144 soil core samples from two pairs of primary and secondary forests. For adult plants, df = 1, 19; for spores produced, df = 1, 19; for spores deposited, df = 1, 494; for spores in soil, df = 1, 140; for juvenile plants, df = 1, 19.

history, but history had a stronger influence than light availability on median fecundity in both *D. intermedia* and *P. acrostichoides*. *Dryopteris intermedia* populations had 20% higher median fecundity and *P. acrostichoides* populations had 50% higher median fecundity in secondary forests than in primary. Despite greater population or individual fecundity, however, no species had greater total spore production in secondary forests, due to lower population densities there (Table 1). In fact, *D. intermedia* and *P. acrostichoides* produced more spores per area in primary forests.

Spore dispersal and the spore bank

Both *D. intermedia* and *P. acrostichoides* deposited significantly greater numbers of spores in primary forests than in secondary, about three times as many on average, while *D. carthusiana* had low levels of spore deposition throughout the two sites (Table 1, Fig. 2A). Within secondary forests, spore abundance appeared to decline with distance from the land-use boundary for *D. intermedia* (F = 3.69, df = 1, 243, P = 0.0560) and *P. acrostichoides* (F = 2.87, df = 1, 242, P = 0.0914; Fig. 2A). Still, a mean of 5100 *D. intermedia* and 8800 *P.*

TABLE 2. Effects of land-use history on individual plant size, reproductive status, and fecundity of three fern species in central New York forests.

	Dryopteris carthusiana			*Dryopteris intermedia*			*Polystichum acrostichoides*		
Source	Effect direction	F/χ^2	P	Effect direction	F/χ^2	P	Effect direction	F/χ^2	P
Size (leaf area)									
History	+	16.3	<0.0001	+	23.7	<0.0001	+	64.0	<0.0001
Odds of reproduction									
History	+	4.72	0.0298	+	2.74	0.0976	+	11.3	0.0008
Size	+	265	<0.0001	+	612	<0.0001	+	281	<0.0001
Fecundity (leaf area with sori)									
History		0.04	0.8438		1.78	0.1829	+	33.3	<0.0001
Size	+	305	<0.0001	+	952	<0.0001	+	238	<0.0001

Notes: Mixed models include site as a random factor to account for the pairing between adjacent stands and agricultural history as a binary variable with 0 = primary forest and 1 = secondary forest. Thus, a positive effect of history indicates a higher value in secondary forests. Directions of effects are shown when $P < 0.10$. Individual size and fecundity were natural-log-transformed. The analyses include only sites with five or more individuals in both stands (N = 11 pairs for *D. carthusiana*, 16 for *D. intermedia*, and 10 for *P. acrostichoides*).

TABLE 3. Effects of land-use history and environmental conditions on population performance of three fern species in central New York forests. Measures of population performance include median plant size, the proportion of plants that were reproductive, and the median fecundity of reproductive plants.

	Dryopteris carthusiana			*Dryopteris intermedia*			*Polystichum acrostichoides*		
Source	Effect direction	*F*	*P*	Effect direction	*F*	*P*	Effect direction	*F*	*P*
Median size (leaf area)									
History		1.53	0.2621		2.34	0.1542		1.62	0.2597
pH		0.43	0.5369		0.31	0.5884		0.78	0.4178
OM		0.44	0.5308		2.13	0.1721	+	5.72	0.0623
Light	+	4.34	0.0823	+	4.92	0.0484		3.79	0.1091
Proportion reproductive (%)									
History	+	10.7	0.0172	+	12.0	0.0053	+	11.4	0.0198
pH		1.60	0.2534		1.07	0.3226		3.32	0.1282
OM		0.79	0.4082		2.46	0.1450	+	21.3	0.0058
Light	+	8.26	0.0283		1.47	0.2513	+	28.4	0.0031
Median fecundity (leaf area with sori)									
History		0.05	0.8285	+	6.44	0.0275	+	14.0	0.0135
pH		0.56	0.4831		0.03	0.8610		0.04	0.8554
OM		1.43	0.2768		1.47	0.2511	+	5.18	0.0720
Light	+	13.5	0.0104		2.65	0.1319	+	11.1	0.0209

Notes: As in Table 2, mixed models compare adjacent stands, and positive effects of history represent higher values in secondary forests. Directions of effects are shown when $P < 0.10$. No interactions were significant at $\alpha = 0.05$. The analyses include only sites with five or more individuals in both stands and exclude one site with exceptionally high performance measures for its low light levels ($N = 10$ pairs for *D. carthusiana*, 15 for *D. intermedia*, and 9 for *P. acrostichoides*). The outlier (WG3) had a dense understory of woody plants below a relatively open canopy. For *Dryopteris carthusiana*, df = 1, 6; for *Dryopteris intermedia*, df = 1, 11; for *Polystichum acrostichoides*, df = 1, 5.

acrostichoides spores/m^2 reached 25 m into secondary forests where adult plants were sparse or absent. In the soil, *D. carthusiana* and *D. intermedia* had similar numbers of spores throughout the primary and secondary forests (Table 1, Fig. 2B). The density of *P. acrostichoides* spores, however, averaged twice as high in primary forest soils as in secondary and tended to decrease with distance from the primary forests ($F = 3.22$, df = 1, 68, $P = 0.0772$; Fig. 2B). Soils of secondary forests without adult plants nevertheless produced 1900 *P. acrostichoides* sporophytes/m^2, or four to five orders of magnitude more than adult population densities.

Gametophyte and sporophyte establishment

In the spore-sowing experiment, covers providing elevated humidity had the greatest impact on the formation and maintenance of both gametophytes and sporophytes (Figs. 3 and 4; for statistical results, see Appendix C). Accounting for all other factors, plots at elevated humidity were approximately 4000 times more likely to have gametophytes, and plots with gametophytes at elevated humidity were 60 times more likely to have sporophytes than plots with gametophytes at ambient humidity. Of plots at elevated humidity, 84% had gametophytes and 51% formed sporophytes, whereas only 12% of open plots had gametophytes and 5% formed sporophytes. The next largest influence on whether plots produced gametophyte and sporophyte plants was the substrate. Gametophyte occurrence was 33 times more likely on mineral soil than on humus and 11 times more likely on humus than on leaf litter. Likewise, given gametophytes at elevated humidity, sporophyte formation was 380 times more likely on mineral soil than on humus and 20 times more likely on humus than on leaf litter. Where sporophytes were present, plots with elevated humidity, mineral soil, and humus also formed greater numbers of sporophytes.

Though the effects of sowing spores were one to three orders of magnitude smaller than the effects of humidity and substrate, establishment rates differed significantly among the three species (Fig. 3). Plots with added *D. carthusiana* or *D. intermedia* spores were two to four times more likely to have gametophytes than either *P. acrostichoides* or unsown control plots. Pairwise contrasts showed no significant differences in gametophyte occurrence between *D. carthusiana* and *D. intermedia* or between *P. acrostichoides* and the unsown control. *Dryopteris carthusiana* also had the highest rate of sporophyte formation, followed by *D. intermedia*, *P. acrostichoides*, and unsown plots. Given gametophytes at elevated humidity, *D. carthusiana* was four to six times more likely to have sporophytes than either *P. acrostichoides* or the unsown control, while other species pairs did not differ significantly. Thus, adding spores enhanced gametophyte formation in *D. carthusiana* and *D. intermedia* and sporophyte establishment rates in *D. carthusiana* but had no effect on either for *P. acrostichoides*. After three years, unsown control plots were no less likely to have sporophytes than plots to which spores of any species had been added. Among plots with sporophytes, all spore-sown plots had higher sporophyte numbers, a mean of 4000 sporophytes/m^2, than the unsown control, with 2500 sporophytes/m^2 (Fig. 4). Still, given suitable conditions, areas without added

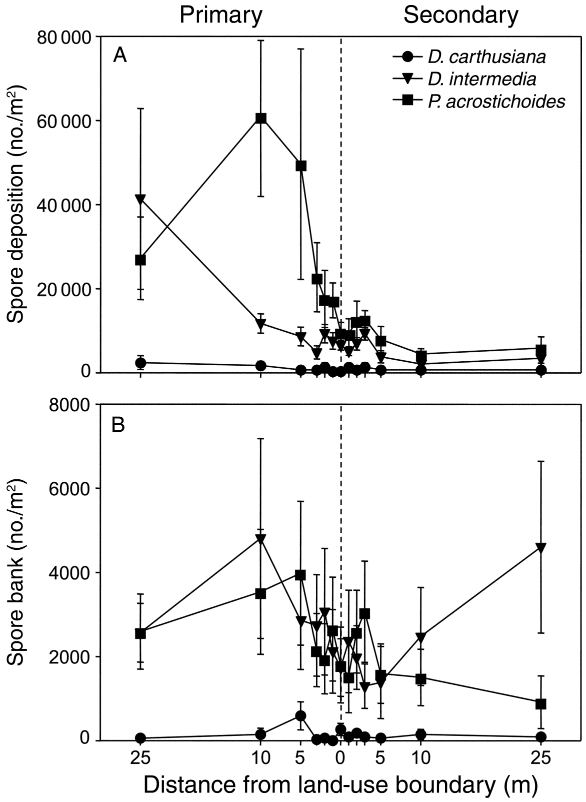

FIG. 2. Spore deposition and the spore bank of three fern species (*Dryopteris carthusiana*, *Dryopteris intermedia*, and *Polystichum acrostichoides*) in two pairs of adjacent primary and secondary forests. At varying distances from the land-use boundary, symbols for each species show (A) the density of spores deposited over one full growing season and (B) the density of sporophytes produced by soil cores (mean ± SE). Note the 10-fold difference in scales.

spores had the capacity to produce stands of sporophytes four to five orders of magnitude more dense than adult fern populations in these forests (Table 1). Sporophyte numbers were similar among the three species, though *D. carthusiana* plots had marginally higher numbers of sporophytes than *P. acrostichoides* (pairwise contrast, $F = 3.37$, df = 1, 169, $P = 0.0682$).

Forest history had no effect on gametophyte occurrence or sporophyte establishment. The analyses also did not detect any significant interactions among the treatments, indicating, for example, that elevated humidity enhanced the odds of establishment on all substrates equally and that the three species and the unsown control responded similarly to the humidity levels and substrates.

Juvenile plant distribution in relation to microhabitat

In surveys of all sites, densities of juvenile plants were generally one order of magnitude less than adult plant densities and did not differ significantly between primary and secondary forests (Table 1). Juvenile *D. carthusiana* plants occurred preferentially on mineral soil, wood, and in moss ($G = 120.2$, df = 6, $P < 0.0001$; $N = 37$); *D. intermedia* occurred preferentially on humus, mineral soil, wood, and in moss ($G = 796.7$, df = 6, $P < 0.0001$; $N = 253$). *Dryopteris carthusiana* and *D. intermedia* had similar distributions across the substrates, with most juvenile plants growing on wood (40%) or mineral soil (33%). In *D. carthusiana* and *D. intermedia*, 48% of juvenile plants were associated with rotten logs and an additional 29% with living tree roots, whether directly on the wood or in crevices created by it. Only 5% grew on treefall mounds and 5% on substrates exposed by water. In contrast, *P. acrostichoides* occurred preferentially on humus and mineral soil and with moss and less often than expected on wood ($G = 1111$, df = 6, $P < 0.0001$; $N = 244$). Most juvenile *P. acrostichoides* plants grew in moss (51%) or on mineral soil (38%). While 18%

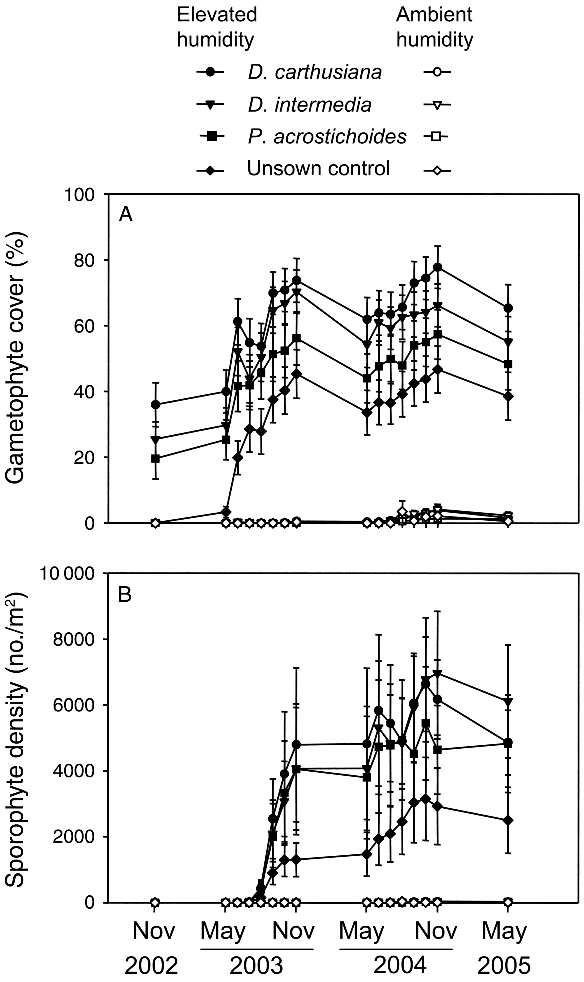

FIG. 3. (A) Gametophyte cover and (B) sporophyte density during a three-year field experiment, in plots sown with spores of three fern species (*Dryopteris carthusiana*, *Dryopteris intermedia*, and *Polystichum acrostichoides*) and unsown control plots, at either elevated or ambient humidity (mean ± SE). For clarity, the figure shows only plots on mineral soil ($N = 240$). At ambient humidity, both gametophyte cover and sporophyte density were low but nonzero.

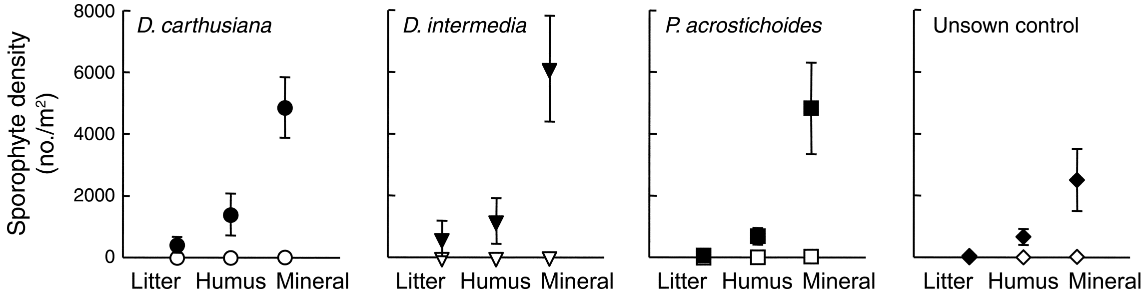

FIG. 4. Sporophyte establishment three years after sowing spores of three fern species (*Dryopteris carthusiana*, *Dryopteris intermedia*, and *Polystichum acrostichoides*) and an unsown control, on leaf litter, humus, or mineral soil, at elevated humidity (solid symbols) or ambient humidity (open symbols; mean ± SE; $N = 720$ plots). At ambient humidity, no sporophytes grew on leaf litter, and sporophyte density was low but nonzero on humus and mineral soil.

were associated with rotten logs and 11% with tree roots, 21% occurred on treefall mounds and 16% on substrates exposed by water. Primary and secondary forests differed significantly in the proportions of forest floors covered by various substrates ($G = 385.2$, df = 6, $P < 0.0001$; $N = 16\,000$). Features more common in primary forests included humus, exposed tree roots, treefall pits and mounds, and pools and rivulets of water (Table 4).

DISCUSSION

This study assessed the status and distribution of plants at a single point in time and quantified the density of individuals in each life history stage. These data support qualitative inferences about the relative importance of each life cycle stage to population growth and spread. In addition, this paper presents the first experiment to examine fern establishment in natural habitats. By planting and following populations of gametophytes and young sporophytes in various microsites for three years, the experiment distinguished whether spore or microsite availability limited establishment in the three species and the two forest types. Since the study did not mark and follow individual plants over time, however, it cannot directly estimate population growth rates. To test the interpretations of population processes drawn here, future work could adapt the methods of this study to make traditional demographic observations on fern gametophytes and young sporophytes and combine these with long-term monitoring of adult plants.

Which life stage limits colonization of secondary forests?

Contrary to predictions based on their distribution, adult plants of all three fern species had similar or greater size and fecundity in secondary forests than in adjacent primary forests. This pattern could arise either because plants in secondary forests are older or because plants of the same age are larger and more reproductive. Since populations in secondary forests likely established within the last 80 years, whereas populations in primary forests may have persisted for thousands of years, plants in secondary forests seem unlikely to be consistently older. A lack of recruitment in secondary forests could contribute to lower proportions of small, pre-reproductive individuals in secondary-forest populations. However, an age difference cannot fully account for the observed performance variation, since individual plant allocation patterns also differed between the forest types. In both *D. carthusiana* and *P. acrostichoides*, plants of the same size were more likely to produce spores in secondary forests, and in *P. acrostichoides*, reproductive plants of the same size produced more spores. These patterns demonstrate that plants respond differently to habitats created by past agriculture and suggest that some aspect of the environment improves performance in secondary forests relative to adjacent primary stands.

Among the measured environmental variables, light availability had the greatest impact on all aspects of population performance for all three species. Light is often a limiting resource in forest understories (Neufeld and Young 2003) and can control the growth and sexual reproduction of other ferns and forest herbs (Hughes et al. 1988, Hill and Silander 2001). In these 20 pairs of

TABLE 4. Percentages (mean ± SE) of primary and secondary forest floors covered by various substrates and larger features.

Cover type	Primary	Secondary	t	P
Substrates				
Leaf litter	77.4 ± 2.65	76.2 ± 4.47	0.34	0.7361
Humus	4.06 ± 0.42	1.66 ± 0.35	5.22	<0.0001
Mineral soil	6.54 ± 1.62	10.64 ± 3.59	−1.67	0.1117
Wood	8.26 ± 0.59	8.65 ± 0.64	−0.59	0.5644
Stone	1.49 ± 0.47	0.68 ± 0.24	1.43	0.1697
Moss	2.18 ± 0.63	2.16 ± 0.51	0.02	0.9806
Grass	0.13 ± 0.09	0.04 ± 0.03	0.92	0.3672
Larger features				
Logs	7.10 ± 0.59	8.15 ± 0.68	−1.67	0.1118
Tree roots	3.41 ± 0.49	2.19 ± 0.22	2.41	0.0261
Pits and mounds	3.21 ± 0.48	0.23 ± 0.09	6.09	<0.0001
Water	2.60 ± 0.77	0.60 ± 0.35	2.41	0.0264

Notes: Percentages represent the proportion of points at which each feature was present, for 400 point samples in each stand ($N = 8000$ for each forest type). Paired t tests compare percentages between adjacent primary and secondary forests ($N = 20$ pairs).

stands, however, adjacent primary and secondary forests have similar understory light availability, as well as similar soil pH, moisture, and physical properties (Flinn and Marks 2007). The most salient difference between the abiotic environments of the two forest types is that secondary forest soils have 15% less OM and 29% less extractable phosphorus than adjacent primary stands (Flinn and Marks 2007). Yet despite this nutrient deficit in secondary forest soils, ferns showed enhanced growth and fecundity there. Evidently these plants provide a more sensitive bioassay of environmental differences between the forest types than direct measurements (Antonovics et al. 1987, Bell et al. 2000), responding to an undetected difference in one of the measured environmental variables or to some unmeasured aspect of the biotic or abiotic environment.

Regardless of its cause, the apparently higher performance of adult plants in secondary forests clearly cannot explain the limited colonization of these stands. Larger, more reproductive plants also seem unlikely to have higher mortality rates. Rather, lower densities of adult plants in secondary forests most likely result from lower recruitment, whether due to reduced spore availability or reduced rates of establishment. Previous studies have shown that most fern spores land within several meters of the parent plant (Peck et al. 1990, Penrod 1994), and in fact, *D. intermedia* and *P. acrostichoides* produced and deposited fewer spores in secondary forests in which adult plants were rare or absent. Spore availability might prove more limiting at greater distances from source populations; in central New York, 90% of secondary forests are adjacent to older stands (Smith et al. 1993). However, this study documented that spores arrive and remain viable in the soil of unoccupied habitats in numbers far in excess of sporophyte recruitment rates. In the field experiment, sowing high densities of spores effectively saturated the plots and produced apparently maximal densities of gametophytes and sporophytes, but a single, full-grown adult plant would fully occupy the same area. The increased rates of gametophyte occurrence with added spores of *D. carthusiana* and *D. intermedia* and the increased sporophyte establishment of *D. carthusiana* thus seem biologically redundant. In the end, unsown plots produced sporophytes as often as plots with added spores of any species and at densities five to six orders of magnitude greater than the observed densities of juvenile plants (Table 1). This result demonstrates that the availability of suitable sites for establishment, not spores, limits recruitment in these populations. In addition, equal rates of establishment in the two forest types indicate that, given similar microhabitat conditions, no other factor reduces recruitment in secondary forests.

Thus, the lower abundance of some species in secondary forests most likely reflects a lack of sites suitable for establishment. Safe sites may be sufficiently rare everywhere that, in 100 years, secondary forests simply have not yet accumulated population densities comparable to the continuously forested primary stands. However, the lower frequency of humus, tree roots, treefall pits and mounds, and ephemeral pools and rivulets in secondary forests has the potential to reduce the recruitment of all three fern species. The different proportions of available microsites suggest a subtle but potentially critical difference in microtopography between the forest types. Plowing leaves the soil surface of secondary forests flat and spatially homogenized; for example, these secondary forest soils also show reduced within-stand variability in soil moisture and pH (Flinn and Marks 2007). Within 20–40 years of abandonment, post-agricultural sites often form a dense thicket of trees or shrubs with a thick and uniform cover of leaf litter, and only the elevated bases and exposed roots of larger and older trees rise above this litter layer. Not until many canopy trees die and fall will these stands begin to redevelop the microtopography typical of long-forested areas. The lack of microtopographic variation in post-agricultural forests could inhibit colonization not only by ferns, but by many other tree and herb species as well (e.g., Harper et al. 1965, Sydes and Grime 1981). On many relevant environmental gradients and spatial scales, then, secondary forests appear to provide suitable habitat for many forest plants, including adults of the three fern species. By examining a type and scale of habitat attributes that others rarely consider, however, this study discovered that agriculture caused persistent reductions in environmental heterogeneity that may continue to hinder plant establishment.

Like most microtopographic variation on the forest floor, microsites that favor fern establishment often result from some form of disturbance, whether large- or small-scale (Werth and Cousens 1990). In this study, larger-scale disturbances associated with juvenile plants included the falling of live and dead trees and branches and soil scouring by water. Though they did not directly observe juvenile plants, several previous studies have documented associations of the *Dryopteris* species with treefall pits and mounds (Beatty 1984, Peterson and Campbell 1993), and McGee (2001) found that *Dryopteris intermedia* had densities twice as high on rotten logs as on the rest of the forest floor. The preferential occurrence of fern gametophytes and young sporophytes on disturbed mineral soil, on rotten wood, and among bryophtes also confirms numerous field observations and anecdotal reports (Cousens et al. 1988, Peck et al. 1990, Groninger and McCormick 1992). In the spore-sowing experiment, extremely small-scale soil erosion both created and destroyed suitable habitats by exposing new patches of bare soil and burying or dislodging small plants. Likewise, earthworms both promoted spore germination by removing leaf litter and turning fresh mineral soil and increased mortality by continually churning the surface; ants and small mammals occasionally played a similar role. Though perhaps more pronounced, a tendency to establish in disturbed microsites is certainly not unique to ferns; even among plants of relatively stable habitats, other spore-bearing and light-seeded species might be expected to share similar requirements (Grubb 1988). In post-agricultural forests, the development of disturbance regimes may thus be integral to the recovery of plant communities.

Which characteristics explain the species' contrasting distributions?

At most life stages, the three fern species showed largely similar responses to land-use history and environmental conditions, but several results suggest that *Polystichum acrostichoides* may have more specific habitat requirements than the *Dryopteris* species. First, its performance showed greater sensitivity to soil conditions, increasing with soil OM. The current 15% soil OM deficit in secondary forests does not appear to hinder plant size or fecundity, since both were greater in secondary forests than in primary. However, cultivation would have initially reduced soil OM by approximately 30%, and soils may have only recently regained current OM levels (Murty et al. 2002). The response of *P. acrostichoides* to this gradient could suggest that soil conditions were less favorable for this species during the development of post-agricultural forests. Second, though the spore-sowing experiment did not detect differences among species in establishment requirements, the natural distribution of juvenile plants suggested that *P. acrostichoides* had a stronger association with mineral soil and moss than the *Dryopteris* species, which occurred equally frequently on wood. Mineral soil and moss were equally common on primary and secondary forest floors, but this pattern could reflect a greater specificity in the response of *P. acrostichoides* gametophytes or juvenile sporophytes to other aspects of their microhabitat.

Whether or not the three fern species have different interactions with post-agricultural environments, their different distributions may also reflect intrinsic life history characteristics. In the spore-sowing experiment, the species' establishment rates fell in the rank order predicted by their distributions, with *D. carthusiana* consistently having the highest rates of gametophyte and sporophyte formation and *P. acrostichoides* the lowest. Sporophyte establishment depends in part on gametophyte mating patterns, which I assessed by growing gametophytes in isolation and in pairs of varying relatedness (Flinn 2006). Results from this laboratory experiment matched those from the field; *D. carthusiana* gametophytes again had the greatest sporophyte production across all treatments, as well as the greatest potential for self-fertilization, while *P. acrostichoides* had the lowest reproductive success and the lowest tolerance for inbreeding. High establishment rates, including the ability to self-fertilize, appear to facilitate rapid colonization in *D. carthusiana*, while lower rates of gametophyte and sporophyte formation, due in part to a predominantly outcrossing mating system, slow the colonization process for *P. acrostichoides* (Soltis and Soltis 1990, Flinn 2006). On a spectrum of life history variation from fast to slow demographic rates and colonization dynamics (sensu Franco and Silvertown 1996, Vellend et al. 2006), it seems that *D. carthusiana* has the fastest rates of the three species, *D. intermedia* is intermediate, and *P. acrostichoides* is simply slower. The basic life history constraints and reproductive biology of these species could thus provide a sufficient explanation for their relative colonization success.

Implications for post-agricultural recovery and community assembly

Since adult survival and growth have the greatest influence on population growth rates in long-lived, perennial plants (Franco and Silvertown 1996), parity in adult performance is an important condition for population persistence in secondary forests. Most forest understory plants investigated so far had similar or better performance in secondary forests relative to primary (Donohue et al. 2000, Verheyen and Hermy 2004), and some species showed higher growth rates (Fraterrigo et al. 2005) or greater reproductive output (Endels et al. 2004). Also as in this study, Fraterrigo et al. (2005) found different allocation patterns between the forest types, with plants in previously farmed stands allocating proportionately more to leaves vs. stems. By contrast, *Trillium grandiflorum* plants at high-pH sites in central New York were smaller and less likely to flower in secondary forests than in primary (Vellend 2005). Even within the same landscape, therefore, individual species have unique responses to the legacies of past agriculture. The accumulated evidence demonstrates that the effects of agriculture on forest understory plants include not only a reduction in species richness, but also a selective, environmental filter that shapes the composition of recovering communities.

Though previous research on herbaceous species in forests regrowing after agriculture focused overwhelmingly on dispersal (reviewed by Flinn and Vellend 2005), this study reveals a greater role for environmental interactions in the process of recolonization. For the three fern species in this study, specific requirements for establishment appear to exclude plants from otherwise favorable habitats and may largely determine population growth rates and species distributions. Similar processes may control the distributions of other spore-bearing and light-seeded species, and establishment requirements could prove increasingly important to tree and herb populations as their seeds accumulate. In fact, establishment limitation is among the strongest filters on recruitment for many temperate forest plants (Clark et al. 1998, Caspersen and Saprunoff 2005). Importantly, though, the environmental attributes that proved critical to fern colonization were not mean positions on environmental gradients, but the microtopographic variation created by disturbance, lending support to the idea that environmental heterogeneity facilitates the maintenance of diversity at local scales.

The microsite-limited recruitment of ferns provides a counter-example to the limitation of recruitment by seed availability and dispersal, which is otherwise widespread among trees and herbaceous plants (Clark et al. 1998, Ehrlén and Eriksson 2000, Turnbull et al. 2000, McEuen and Curran 2004). It demonstrates that different processes control the distributions of different species within the same guild, and the relative influences of these processes appear to depend largely on species' life histories. Among species with low fecundity and short-distance dispersal, relative colonization success often depends on fecundity and dispersal-related traits (Matlack 1994, Verheyen et al. 2003). The distributions of ferns and other well-dispersed species may depend instead on atttributes that determine establishment rates, but similarly reflect life history traits related to colonization ability. Despite the prominent role of dispersal limitation in the development of post-agricultural communities, this process clearly contrasts with models of random dispersal assembly. Rather, the life histories of individual species are manifest in the unique mechanisms that determine their dynamics and distributions.

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APPENDIX A

Table of regression equations used to estimate leaf area and spore production from simple field measurements of fern plants (*Ecological Archives* E088-192-A1).

APPENDIX B

Additional details of methods used (*Ecological Archives* E088-192-A2).

APPENDIX C

Statistical analysis of spore-sowing experiment (*Ecological Archives* E088-192-A3).