

INVASIBILITY AND ABIOTIC GRADIENTS: THE POSITIVE CORRELATION BETWEEN NATIVE AND EXOTIC PLANT DIVERSITY

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Abstract. We sampled the understory community in an old-growth, temperate forest to test alternative hypotheses explaining the establishment of exotic plants. We quantified the individual and net importance of distance from areas of human disturbance, native plant diversity, and environmental gradients in determining exotic plant establishment. Distance from disturbed areas, both within and around the reserve, was not correlated to exotic species richness. Numbers of native and exotic species were positively correlated at large (50 m²) and small (10 m²) plot sizes, a trend that persisted when relationships to environmental gradients were controlled statistically. Both native and exotic species richness increased with soil pH and decreased along a gradient of increasing nitrate availability. Exotic species were restricted to the upper portion of the pH gradient and had individualistic responses to the availability of soil resources. These results are inconsistent with both the diversity-resistance and resource-enrichment hypotheses for invasibility. Environmental conditions favoring native species richness also favor exotic species richness, and competitive interactions with the native flora do not appear to limit the entry of additional species into the understory community at this site. It appears that exotic species with niche requirements poorly represented in the regional flora of native species may establish with relatively little resistance or consequence for native species richness.

Key words: *alien species; community invasibility; community saturation; diversity; exotic species; fluctuating resource hypothesis; invasive species; niche; resistance; resource enrichment hypothesis.*

INTRODUCTION

Invasive species have attracted considerable attention both because of their adverse impacts on natural ecosystems (Mack et al. 2000) and their relevance to tests of theory in community ecology (Tilman 1993, 1997, Levine 2000, 2001, Davis et al. 2001, Moore et al. 2001). Explanations of plant invasions have predicted invasibility on the basis of the invader's traits (e.g., Kolar and Lodge 2001, Mack 2003), the invading plant's ecological relationships in a new environment (Keane and Crawley 2002), and the competitive effects of the native plant community (Davis et al. 2001, Levine 2001, Moore et al. 2001, Kennedy et al. 2002). The two most prominent conceptual models of plant community invasibility are the diversity-resistance hypothesis (Elton 1958, Kennedy et al. 2002) and the resource-enrichment hypothesis (Davis et al. 2000). The diversity-resistance hypothesis builds on assumptions about niche overlap and competitive exclusion to argue that, all else being equal, communities with high native diversity are less invulnerable (Kennedy et al. 2002). The resource-enrichment hypothesis, also called the fluctuating-resources hypothesis, assumes that exotic species are resource limited, and hence, that communities "become more susceptible to invasion whenever there is an increase in unused resources," such as after a disturbance (Davis et al. 2000). Both hypotheses assume that the success of exotic species is dependent on resource availability, either directly (resource-enrichment) or indirectly due to competition with native species having similar niches (diversity-resistance). Evidence for these hypotheses is mixed, with experimental evidence generally supporting the diversity-resistance hypothesis (Tilman 1997, Levine 2000, 2001, Kennedy et al. 2002), and sampling of natural assemblages showing the opposite, with a positive correlation between native and exotic species richness (e.g., Lonsdale 1999, Sax 2002, Meiners et al. 2004). A positive relationship between exotic and native diversity is not inconsistent with the resource-enrichment hypothesis, but these studies have not directly tested the hypothesis by quantifying resource availability in relation to plant distributions (but see Brown and Peet 2003).

Two additional factors affecting invasion success in plant communities have emerged from previous studies. First, dispersal of exotic seeds from external sources can be important independently or in conjunction with environmental factors (Levine 2000, Rouget and Richardson 2003), but may decrease in importance as invading species colonize an area and dispersal becomes less limiting (Wiser et al. 1998). A second con-

Manuscript received 24 June 2004; revised 29 September 2004; accepted 10 December 2004. Corresponding Editor: K. D. Woods.

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sideration is the degree to which the native community is unsaturated, or lacks diversity due to a limited regional pool of species (Tilman 1997, Sax and Brown 2000, Moore et al. 2001, Dupré et al. 2002, Ricklefs 2004, Shurin and Srivastava, *in press*). For example, the widely divergent tree species diversity between the temperate zones of eastern Asian, eastern North America, and Europe may be due to differences in the history of these continental floras rather than to interactions among species in a given region (Latham and Ricklefs 1993, Ricklefs et al. 2004). Even where local diversity is relatively high, portions of resource gradients may be floristically unsaturated because species able to exploit that combination of resources have been lost over time or never evolved in the region (Sax and Brown 2000, Ricklefs 2004). The currently dominant hypotheses for invasibility do not consider impoverishment of the regional species pool, even though theoretical analyses (Moore et al. 2001) suggest this may be a critical shortcoming for the diversity-resistance hypothesis in particular. To fully evaluate the alternative explanations for invasibility, we need to simultaneously assess native species richness, environmental gradients, seed-rain, and community saturation.

In this paper, we try to disentangle the factors influencing the establishment of exotic species in the understory of an old-growth, temperate forest. We test whether: (1) proximity to disturbed areas increases exotic species richness and abundance, (2) exotic species richness decreases as native species richness increases, as predicted by the diversity-resistance hypothesis, and (3) exotic species richness increases with increased availability of limiting resources, as predicted by the resource-enrichment hypothesis.

METHODS

The 10-km² Gault Reserve is a complex of low, forested hills surrounded by agricultural and suburban development near Montréal, Québec (45°31' N, 73°08' W; more information *available online*).² The site, which has been protected from exploitation and settlement since the arrival of the Europeans in this region, is the largest and best-preserved primary forest remnant in the St. Lawrence River Valley. The reserve has diverse forest communities (Maycock 1961, Arie and Lechowicz 2002, Arie et al. 2005), but the most common canopy trees are *Acer saccharum* Marsh. (35% projected cover), *Fagus grandifolia* Ehrh. (20%), and *Quercus rubra* L. (19%). While all but a few isolated localities within this extensive tract of primary forest have been protected from human disturbance, the forest is subject to natural disturbance by glaze ice storms that can damage the forest overstory and that recur at 20- to 100-year intervals (Hooper et al. 2001).

We used a digital elevation model of the reserve to stratify potential sampling sites among environmental

classes based on terrain attributes (aspect, slope steepness, and slope position; cf. Grigal et al. 1999). We took these physiographic variables as indicators of site hydrology, insolation, and nutrient availability, which were to be measured later. In choosing potential sampling sites, we included only old-growth forest and excluded water bodies, areas within 10 m of trails, the shore of Lac Hertel inside the reserve, and areas within 15 m of the outer perimeter of the reserve. Our sampling design (Gilbert and Lechowicz 2004) decouples the usual correlation between distance and environmental similarity, so that sites closer together are not on average more similar to each other than those further apart. For example, south-facing, steep, mid-slope sites were chosen such that both similar and dissimilar sites were evenly distributed across the range of between-site distances. We assessed selected sites in early 2002 to ensure that the topographic characterization was accurate and iteratively used Mantel tests of initial field estimates of slope, aspect, soil moisture, and humus richness to ensure that there indeed was no detectable correlation between inter-site distances and site similarities. This sampling design allows us to explicitly account for the influence of resources on species richness and also to test the independent effects of migration of exotic plants into the reserve from disturbed areas.

Between 15 May and 30 July 2002, the fifth growing season after the last major ice storm, we sampled the ground layer community of herbaceous and woody species in the reserve. We sampled 50-m² circular plots with nested plots of 10 m². This nested sampling design is important for assessing effects of within-site heterogeneity that can confound the relationship of native to exotic species diversity (Shea and Chesson 2002). We estimated percent cover for each vascular plant species under 1.5 m tall within each plot. Nomenclature and species origins (native or exotic) follow Gleason and Cronquist (1991), with species counted as exotic if they were not of North American origin. We pooled four soil cores, taken in August 2002 to a depth of 8 cm, for analysis of soil nutrients, pH, and loss on ignition in each plot (Gilbert and Lechowicz 2004). Following seven days without rain, we estimated soil moisture regime over two days in early September 2002, using three measurements in each plot to a depth of 5 cm with a Delta-T Devices theta probe (type ML2x, Cambridge, UK). This provided an index of the relative soil moisture among plots. We used GLA software (Frazer et al. 1999) and hemispherical photographs taken 1 m above the ground in August 2002 at the center of each plot to determine direct, indirect, and total irradiance. We combined these three measures of irradiance using a principal components analysis (PCA), with the first axis, representing 95.8% of the variation, taken to represent the light regime. Thus, the complete set of environmental variables used in subsequent analyses consisted of light regime, slope steepness, soil pH, and the

² (www.mcgill.ca/gault)

TABLE 1. Species by group, with percent cover and presence statistics.

| Species group | No. species | Maximum cover by one species in a single 50-m ² plot (%) | Total cover of median species (%) [†] | Maximum no. plots occupied by one species | Median no. plots occupied |
|----------------|-------------|---|--|---|---------------------------|
| Graminoids | 43 | 55 | 1.1 | 30 | 3 |
| Herbs | 90 | 60 | 2 | 37 | 4 |
| Pteridophytes | 29 | 38 | 8 | 40 | 4 |
| Shrubs | 22 | 20 | 6.4 | 26 | 6 |
| Tree seedlings | 20 | 55 | 5.4 | 64 | 7.5 |
| Exotic species | 12 | 7 | 0.6 | 23 | 2 |

[†] Based on total percent cover of each species.

logarithmic transformations of soil moisture, soil loss on ignition, P, NO₃, NH₄, K, Mg, and Ca.

Distance from the nearest trail, access road, or developed site (picnic area, buildings, an old orchard) within the reserve boundaries, as well as distance from the outer perimeter of the reserve (e.g., Honnay et al. 2002), were used to model distance from areas of human disturbance that might serve as source areas for dispersal of exotic plants. Many exotic plant species (e.g., *Alliaria petiolata*, *Cirsium arvense*, *Hypericum perforatum*, *Plantago major*, *Rumex obtusifolius*, *Taraxacum officinale*, *Tussilago farfara*) have substantial populations on suburban and agricultural land adjacent to the reserve or in the few developed areas within the reserve (M. J. Lechowicz, unpublished data). Distances were calculated using GIS overlays of site positions, trail and road systems, and the reserve boundary, and both linear and log-transformed distances were used in our analyses (Gilbert and Lechowicz 2004).

STATISTICAL ANALYSES

We performed regression analyses and a canonical correspondence analysis to test expectations based on the prevailing hypotheses for invasibility and their underlying assumptions. All analyses were performed with data from the larger (50 m²) plots, with analyses of the smaller, nested plots used only to assess the consistency of the relationship between native and exotic species richness. We tested for predicted trends (1) with general linear models, using a Poisson distribution, as this model fit the underlying distribution of our data; and (2) with multiple linear regressions (MLR). The two types of analysis gave similar results, and we report the MLR results.

MLR analyses were used to assess our original predictions by testing for: (1) an effect of distance from disturbance on exotic species richness, (2) a relationship between exotic and native species richness, and (3) effects of environment on exotic and native species richness. Due to the influence of the environment on exotic species richness, both tests 1 and 2 were also performed on the residuals of the environment to exotic species relationship to ensure that, under similar environmental conditions, the correlation between native and exotic species richness was consistent. Logarithmic

or quadratic transformations were used on all variables, as necessary, to linearize relationships. All regressions were performed in SAS system 8.1, with the maximum R method used in MLR to determine the best models at $\alpha = 0.05$ (SAS Institute 1999).

Prior to MLR analysis of environmental effects, we performed a PCA of standardized environmental data to generate orthogonal environmental gradients (Legendre and Legendre 1998). The MLRs of the original environmental gradients and the PCA axes gave almost identical results, and we therefore only consider the original variables further.

We used Canonical Correspondence Analysis (CCA; Legendre and Legendre 1998, ter Braak and Smilauer 1998) to model the distribution of exotic species abundances along environmental gradients (Legendre and Legendre 1998). We used the original environmental variables as explanatory variables in the CCA along with two interaction terms, nitrate \times soil moisture and ammonium \times soil moisture. We excluded exotic species that occurred in fewer than two sites. All variables were subjected to forward selection ($\alpha = 0.05$). Examination of the CCA scattergram showed no arch effect, which indicates that all axes can be used to interpret species' distributions and the explanatory power of the model (Legendre and Legendre 1998).

RESULTS

A total of 215 species occurred in our plots, 12 (5.6%) of which were exotic (Table 1); all 12 exotics are of European origin and their environmental affinities in central Europe are well known (Table 2; Ellenberg et al. 1991). Native species richness and cover within plots ranged from 7 to 44 species and 7% to 94%, respectively. Exotic species richness within plots ranged from 0 to 5 (median 1), and cover ranged from 0% to 7% (median 0.1%). Although some exotic species were widespread, exotics did not dominate in any plot (Tables 1 and 2).

Exotic species richness showed a significant positive trend ($P < 0.02$, $df = 67$) with distance from the reserve perimeter, opposite to expectation. This effect was not significant when distance was tested against the residuals of the exotic species to environmental gradients relationship ($P > 0.05$, $df = 67$); environmental con-

TABLE 2. Exotic species, with percent cover, presence statistics, and Ellenberg values indicating environmental affinity.

| Species | Maximum cover in any plot (%) | Total cover across all plots (%) | Rank based on total abundance† | No. plots occupied | Rank based on no. plots‡ | Ellenberg values§ | | | |
|------------------------------|-------------------------------|----------------------------------|--------------------------------|--------------------|--------------------------|-------------------|---|---|---|
| | | | | | | R | N | L | F |
| <i>Arctium lappa</i> | 0.2 | 0.2 | 178 | 1 | 185.5 | 7 | 9 | 9 | 5 |
| <i>Barbarea vulgaris</i> | 0.2 | 0.2 | 178 | 1 | 185.5 | 7 | - | 8 | 3 |
| <i>Cerastium vulgatum</i> | 0.1 | 0.1 | 200 | 1 | 185.5 | - | 5 | 6 | 5 |
| <i>Epipactis helleborine</i> | 0.2 | 1.2 | 178 | 11 | 50.5 | 7 | 5 | 3 | 5 |
| <i>Galeopsis tetrahit</i> | 0.1 | 0.2 | 178 | 2 | 142 | - | 6 | 6 | 7 |
| <i>Geranium robertianum</i> | 7 | 7.7 | 69 | 4 | 100.5 | - | 7 | 4 | - |
| <i>Plantago major</i> | 0.1 | 0.1 | 200 | 1 | 185.5 | - | 6 | 8 | 5 |
| <i>Poa compressa</i> | 1 | 1.5 | 121.5 | 5 | 85 | 9 | 2 | 9 | 2 |
| <i>Rumex obtusifolius</i> | 0.8 | 0.9 | 146 | 2 | 142 | - | 9 | 7 | 6 |
| <i>Taraxacum officinale</i> | 0.5 | 3.8 | 92.5 | 23 | 17.5 | - | 7 | 7 | 5 |
| <i>Tussilago farfara</i> | 0.2 | 0.3 | 169 | 2 | 142 | 8 | 6 | 8 | 6 |
| <i>Valeriana officinalis</i> | 0.8 | 1.0 | 139.5 | 3 | 119 | 7 | 5 | 7 | 8 |

Note: Rank includes native species; the number of the rank changes depending on the number of tied scores, with ties being given average rank values.

† Lowest rank = 200, second lowest = 178.

‡ Lowest rank = 185.5, second lowest = 142.

§ Ellenberg values (Ellenberg et al. 1991) provide ordinal coding (1–9) of the species optima along a particular environmental gradient. The letters represent the following gradients: R, soil pH; N, soil fertility; L, insolation; and F, moisture. For each of these gradients, the higher the score, the higher is the level of the resource in the species' realized niche. In other words, a species with an insolation value of 2 would be very shade tolerant relative to a species with an insolation value of 7. Hyphens indicate a broad tolerance (a generalist) rather than a sharp optimum, and all these values reflect niches as realized in central European vegetation.

ditions in the interior of the reserve may favor high exotic-species richness. Distance from trails and other disturbed areas within the reserve also showed no effect on exotic species richness. In this case, exotic species do not appear to be influenced by proximity to areas of human disturbance.

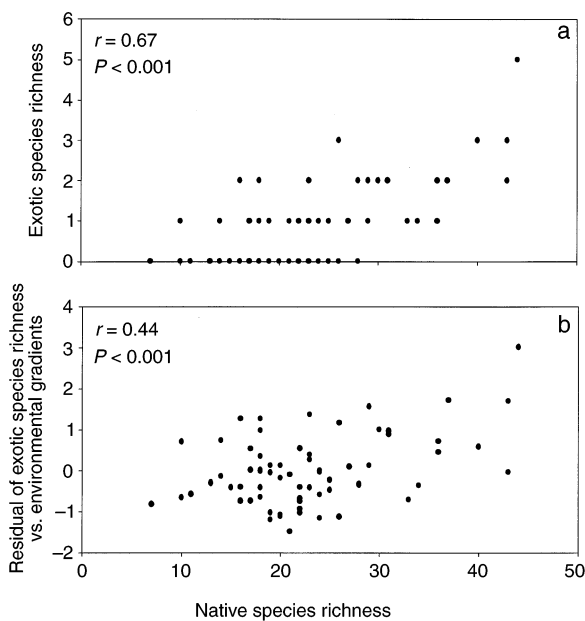


FIG. 1. The correlations (a) between native species richness and exotic species richness and (b) between native species richness and the residuals of exotic species richness once the effect of environmental gradients is removed.

A positive relationship between exotic species richness and native species richness was the strongest correlation observed, and remained even when the effect of the environment was removed statistically (Fig. 1). The converse was not true; residuals from the regression of exotic species richness on native species richness showed no relationship to environmental variables. The 10-m² nested plot also showed a positive relationship between exotic and native species richness, although the trend was slightly weaker ($r = 0.57$, $P < 0.0001$, $df = 67$).

The significant environmental predictors of exotic species richness were pH and NO_3^- , which together explained 30% and 38% of exotic and native species richness, respectively (both $P < 0.0001$, $df = 66$). Both native and exotic richness were positively correlated with pH and negatively correlated with nitrate, with pH explaining approximately twice as much variation in species richness patterns as nitrate.

The following variables produced statistically significant relationships and were included in the CCA: slope steepness, the logarithmic transformations of soil moisture, P, NO_3^- , NH_4^+ , and Mg, and the NH_4^+ by soil moisture interaction. The CCA indicated that optima for exotic species were broadly spaced on environmental gradients (Fig. 2). For example, *Geranium robertianum* was most abundant at moderately high levels of nitrate availability and *Valeriana officinalis* at high soil moisture content. *Poa compressa* and *Taraxacum officinale* were separated on a gradient defined by the interaction between ammonium and water (the third canonical axis), with *T. officinale* peaking on wet, ammonium-rich sites. The CCA explained 64–78% of the

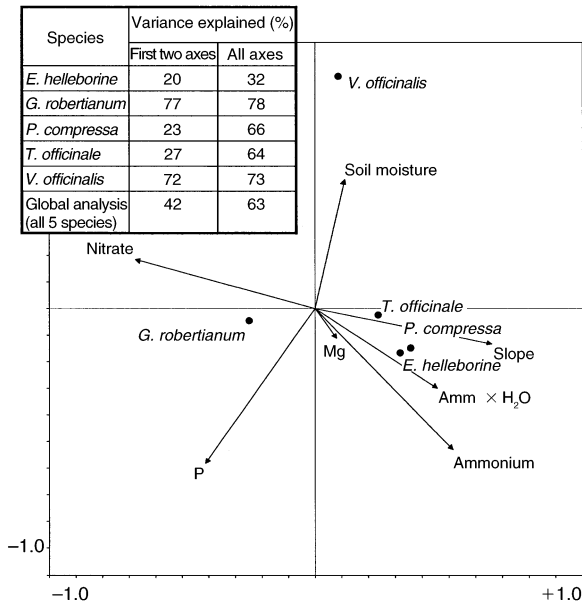


FIG. 2. Biplot of CCA output with species (points) and environmental gradients (vectors) for the most common exotic species sampled. Species abbreviations are the first letter of the genus followed by the species name (see Table 2 for full species names). Amm and H₂O represent NH₄⁺ and soil moisture, respectively; amm × H₂O represents an interaction between NH₄⁺ and soil moisture.

variation in these four species. Although pH is an important predictor of exotic species richness in the MLR analyses, the CCA shows no differentiation of species responses within the relatively narrow range of high pH sites to which all the exotics were restricted. In contrast, exotic species occurred across the full range of ammonium and soil moisture levels sampled in the reserve, and thus showed as much variation with respect to these gradients as native species.

DISCUSSION

The exotic species in this study are not aggressive invaders (White et al. 1993) and were not dominant in any sample plots (Tables 1 and 2). Hypotheses invoking competitive superiority, such as the enemy release hypothesis and evolutionary differences hypothesis (e.g., Keane and Crawley 2002), are unlikely to account for the observed patterns (Daehler 2003).

Distance from disturbed areas was not a significant predictor of exotic species richness. Although a number of studies have shown the importance of exotic seed supply either through direct manipulation (Tilman 1997, Levine 2000, 2001) or through large-scale models (Rouget and Richardson 2003), Wisser et al. (1998) have shown that distance from disturbance can become less important as exotic species establish in an area. Settlement of the area surrounding our study site dates to the 18th century, and many exotics have had ample time to establish in favorable sites within the reserve.

For example, *Geranium robertianum*, a shade-tolerant forest herb (Ellenberg et al. 1991), was reported in similar habitats in this reserve as early as 1877 (Maycock 1961). In addition, on this hill complex standing above agricultural lands on the valley floor, wind may facilitate multidirectional dispersal throughout the reserve. Deer are common in and around the reserve and may also disperse seeds over large distances (Vellend et al. 2003, Myers et al. 2004). *T. officinale* is widespread in the reserve (Table 2), ubiquitous in the seed bank (Leckie et al. 2000), and is known to be dispersed by deer (Myers et al. 2004). It appears that exotic species in the regional species pool have had time and opportunity to disperse throughout the reserve. If dispersal does not limit the distribution of exotics within the reserve, questions concerning effects of resources and competitive environments become primary.

The diversity-resistance hypothesis predicts that competitive interactions should lead to fewer exotic species occurring in parts of the reserve that are richer in native species, but we found the opposite to be true. Other observational studies have noted positive correlations between native and exotic plant richness (Lonsdale 1999, Sax 2002, Sax and Gaines 2003, Meiners et al. 2004), and theoretical analyses have shown that such positive relationships can arise in communities that are not species saturated (Moore et al. 2001). This correlation might indicate that the effect of native species richness in depressing exotic species richness via niche-based competition is overshadowed by a stronger response by both groups to environmental gradients, but this possibility is not supported by our data. Even with the effects of environmental gradients controlled statistically, native and exotic species richness still show a significant positive relationship (Fig. 1). This relationship persists at the spatial scale of the nested 10-m² plots where within-plot environmental heterogeneity can be expected to be lower and effects of competition more apparent. Previous studies also have shown positive correlations between native exotic species richness persisting from larger plot sizes (as in our study) to microsite (0.75–1.0 m²) scale in upland forests (Brown and Peet 2003, Wisser et al. 1998) and in scrub communities (Sax 2002). At the scale of an individual plant, negative interactions between neighbors may well occur, as has been observed in some riparian areas (Brown and Peet 2003), but at the scale of plant neighborhoods (Ennos 2001) in this forest understory the positive relationship between the richness of exotic and native species is unambiguous.

A decisive test of the resource-enrichment hypothesis would require data on temporal resource fluctuation. However, the environmental correlates of exotic species distributions call this hypothesis into question for three reasons. First, both exotic and native species richness are positively correlated with soil pH, consistent with observations that species richness increases along pH gradients in temperate forests (e.g., Brown

and Peet 2003, Peet et al. 2003). Partel (2002) also shows a positive relationship between soil pH and species richness worldwide in mid-latitude forests within the range of pH conditions found at our site ($3.9 < \text{pH} < 7.9$, median 5.5). Since the sort of pH fluctuations required by the resource-enrichment hypothesis are unlikely in well-buffered forest soils and were not evident even in the aftermath of a very destructive ice storm at the site (Hooper et al. 2001, Ariei 2002), it seems likely that some other explanation for variation in the richness of exotic species within the reserve must be found. Second, some resource availabilities did fluctuate in the immediate aftermath of the 1998 ice storm, but the responses of exotic species do not follow expectations under the resource-enrichment hypothesis. Nitrate increased following the last ice storm (Ariei 2002) and is often taken as the limiting factor for plant growth in the understory of temperate deciduous forests (Tessier and Raynal 2003, Campbell et al. 2004), but is negatively rather than positively correlated with the richness of both exotic and native species. Insolation also increased after the 1998 ice storm, but by 2000 insolation in the ground layer had returned to pre-storm levels (Ariei 2002); exotic species favored by high insolation may have established immediately after the storm event, but they have persisted as the ground layer returned to shaded condition. Moreover, the exotics do not occur on low pH sites, where canopy damage from the ice storm was greatest (Ariei and Lechowicz 2000, Ariei 2002, Hooper et al. 2001). The third inconsistency with the resource-enrichment hypothesis is that the exotic species are restricted to different portions of most resource gradients, with the exception of pH (Fig. 2). Thus, an increase in exotic species richness due to a flux in a given resource seems unlikely given the diverse responses of these species to nutrients. The resource-enrichment hypothesis does not provide a satisfactory explanation for the distribution of exotic species in this reserve.

How then can we explain the positive relationship between the richness of native and exotic species, their common increase along soil pH gradients, and their negative correlation with increasing nitrate availability? One plausible explanation is that environmental factors that promote high native diversity also favor establishment of exotic species (Shea and Chesson 2002), and that the native community is not species saturated (Sax and Brown 2000, Moore et al. 2001, Dupré et al. 2002, Ricklefs 2004). In this situation, competitive interactions among native species would not set an upper limit to local diversity and communities can still accommodate additional species without loss of native species. This is consistent with our results, especially with the fact that all the exotics occur at the upper range of pH gradients within the reserve and are either limited to or tolerant of high pH regimes in their native range (Table 2). These exotics originate in a central European flora that is unusually rich in

calcicole species compared to the eastern North American flora (Peet et al. 2003, Ewald 2003, Pärtel 2002). For example, 50–65% of the forest flora of central Europe favors soil pH exceeding 5.5 (the median pH within the reserve), compared to <15% in the Blue Ridge Mountains, suggesting that a relatively limited regional pool of North American calciphilous species may leave the understory community open to colonization by exotic calcicoles. Within the upper portions of the pH gradient, niche segregation does occur but only on other resource gradients (Fig. 2). These realized niches are consistent with the environmental affinities of the exotic species in their native range (Ellenberg et al. 1991; Table 2), and also with other studies done in North America. For example, *Poa compressa* is successful in dry forests in Wisconsin (Whitford and Whitford 1978), and shows little growth response to nitrogen (Taub 2002). We tentatively conclude that the native understory community in the reserve is unsaturated and does not fully exploit available resources; exotic species with appropriate adaptations can successfully colonize under-utilized portions of resource gradients (Sax and Brown 2002, Mack 2003).

In addition, it appears that the understory community in this forest is not nitrogen limited. In light of the typical, hump-shaped relationship between diversity and nitrogen availability (Dupré et al. 2002, Cornwell and Grubb 2003) and given the effects of decades of acid deposition in the region (Campbell et al. 2004), it may be that increases in nitrate cause a decrease in native and exotic species diversity. Studies in grasslands and forests have shown that increases in nitrogen have caused exclusion by increased competition (Turkington et al. 2002, Cornwell and Grubb 2003) or that other resources have become limiting to local diversity (Tessier and Raynal 2003). Possible effects of a depauperate pool of calcicole species, combined with species interactions mediated by interactions on other resource gradients, offer an interesting potential example of the interaction between local and regional processes in determining species diversity (Ricklefs 2004, Shurin and Srivastava, *in press*).

In summary and conclusion, our study uses a novel sampling design to make inferences about processes that determine invasibility in an old-growth forest ecosystem. This approach has led us to four main conclusions. First, distance from areas of human disturbance does not have a measurable influence on exotic species establishment in this reserve. This is likely due to the long history of exotics in the region, the high dispersal ability of some species, and the importance of specific environments in determining individual species' distributions. Second, our results appear to be inconsistent with the resource-enrichment hypothesis, as exotic species richness is negatively associated with a resource that increased in availability after recent disturbance, and positively associated with the upper portions of stable gradients in soil pH. Third, the observed positive

relationship between the richness of native and exotic species is inconsistent with the diversity-resistance hypothesis for the site as a whole, although a diversity-resistance relationship may apply within a restricted portion of the environmental gradients represented in the reserve. Our results are consistent with the possibility that the environmental conditions that promote native species richness also promote exotic species richness, and that competition is not limiting species richness in these conditions. This interpretation suggests that exotic species with niche requirements not well represented in the native flora can colonize this forest understory community with relatively little resistance or consequence for native species.

ACKNOWLEDGMENTS

Samuel Larrivée, Anneli Jokela, Jon Shik, Murielle Vrins, and Greg Gilbert provided field assistance. Soil analyses were done by Claude Camiré at Laval University. Special thanks to Ken Aree, Kate Kirby, Ernest Lo, Jackie Ngai, and Diane Srivastava for comments on the manuscript; Benoit Hamel for GIS support; Pierre Legendre for statistical advice; and Samuel Larrivée, Tyler Smith, and Marcia Waterway for assistance with plant identification. Kerry Woods and three anonymous reviewers made thoughtful critiques of earlier drafts. The Natural Science and Engineering Research Council of Canada provided research (M. J. Lechowicz) and scholarship (B. Gilbert) support.

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