

ENVIRONMENTAL DISTRIBUTION OF FOUR *CAREX* SPECIES (CYPERACEAE) IN AN OLD-GROWTH FOREST¹

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We conducted an in-depth characterization of the range of micro-environments (1 m²) in which four *Carex* species (*C. backii*, *C. communis*, *C. plantaginea*, and *C. platyphylla*) grow in the understory of an old-growth, deciduous forest in southern Québec, Canada. All four species occurred in significantly different micro-environments. *Carex plantaginea* was found at the wet end of a moisture gradient, in soils with high nitrate availability. *Carex backii* and *C. platyphylla* were found at the dry end of the moisture gradient, with *C. backii* occupying soils with higher phosphorus availability than *C. platyphylla*. *Carex communis*, the only ant-dispersed species studied, was found in the broadest range of environmental conditions. Our results suggest that environmental heterogeneity and interspecific microhabitat preferences are important for the maintenance of local species diversity in the forest understory, not only for common species as demonstrated in previous studies, but for infrequent species, and those within a functional group (upland *Carex* species). However, there was some evidence that the distributions of *C. backii* and *C. communis* were not in equilibrium with current environmental conditions, indicating that historical factors, such as dispersal and colonization events, may also have important effects on the distributions of these species and the maintenance of species diversity in old-growth forest.

Key words: *Carex*; Cyperaceae; environmental heterogeneity; forest herbs; habitat niche; sedges; species diversity; understory herbs.

Small-scale environmental heterogeneity and differences among species in their microhabitat preferences are thought to be important factors for the maintenance of local species diversity in temperate forest-herb communities (e.g., Struick and Curtis, 1952; Bratton, 1976a, b; Crozier and Boerner, 1984; Beatty, 1985; Lechowicz, Schoen, and Bell, 1988). Support for this idea has come from demonstrations of interspecific differences in distribution patterns along gradients of soil depth (Bratton, 1976b), slope angle (Pabst and Spies, 1998), microtopography (Bratton, 1976a; Beatty, 1985), soil moisture (Hicks, 1980; Graves and Monk, 1982; Pregitzer and Barnes, 1982), pH (Falkengren-Grerup, 1990), and mineral nutrients (Crozier and Boerner, 1984; Lechowicz, Schoen, and Bell, 1988). However, recent studies on forest herbs in deciduous forests in Sweden have shown several species to be limited as much by dispersal as by specific microhabitat requirements (Eriksson and Ehrlén, 1992), suggesting that stochastic dispersal and colonization events may also be important factors for the maintenance of forest-herb diversity (Fröborg and Eriksson, 1997).

Most of the studies cited above have focussed primarily on the more common species in the forest understory, with com-

munity studies often resulting in a classification of species into functional groups, or guilds, based on microhabitat preferences (e.g., Bratton, 1976a; Hicks, 1980; Graves and Monk, 1982; Pregitzer and Barnes, 1982; Menges and Waller, 1983). Two important aspects of diversity are not accounted for in these studies. First is the within-guild diversity. Huston (1994) has suggested that diversity among functional groups may be maintained by fundamentally different processes than diversity within functional groups. Given that there are often differences among groups of common forest herbs in their distribution along environmental gradients, there is a need to now ask whether functionally similar species that often co-occur also partition the environment in a similar way. The high complexity of environmental gradients in the understory of deciduous forests (Gauch and Stone, 1979; Mann and Shugart, 1983) indicates that a more detailed, multivariate consideration of micro-environmental gradients is the appropriate approach to testing for distributional differences among functionally similar species. Another aspect of diversity, often ignored in studies of forest-herb distribution, is the number of rare or infrequent species, which in fact represent the majority of species in many species-rich plant communities (Grubb, 1986), including the understories of northern deciduous forests (Curtis, 1959; Maycock and Curtis, 1960; Peterken, 1996).

Conclusions drawn from comparative studies can be strengthened by studying closely related taxa, thus minimizing the confounding effect of differences in evolutionary history among species (Harvey and Pagel, 1991). In deciduous forests of eastern North America, the most species-rich genus of plants in the understory is often *Carex*, and many of these species occur infrequently relative to common forest herbs such as *Trillium grandiflorum* and *Erythronium americanum* (Curtis, 1959; Maycock and Curtis, 1960; Walther, 1963; Op de Beek, 1972). Despite their exceptional diversity, forest understory *Carex* species have received remarkably little atten-

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tion in the ecological literature (Bernard, 1990; but see Handel, 1976a, b, 1978a), and many, or all, species are often recorded in vegetation studies simply as *Carex* spp. (e.g., Brewer, 1980; Metzger and Schultz; 1981; Collins and Pickett, 1982).

A community of sedges in an old-growth deciduous forest at Mont St. Hilaire, Québec, where >50 *Carex* species have been recorded, is the subject of ongoing investigations (Bell, Lechowicz, and Waterway, 2000). The distribution of a group of lowland species at Mont St. Hilaire is distinct from that of a group of upland species, with one species, *Carex plantaginea* Lam., not associated with either of these groups. Most species at Mont St. Hilaire belong to the upland group, but little is known about the relationship between environment and distribution patterns among species within this group. This presents an ideal opportunity to ask whether the pattern of environmental partitioning previously demonstrated for groups of frequently encountered species also applies to relatively infrequent, functionally similar species growing in a common habitat. Given that the herbaceous layer in second-growth forests of eastern North America may take many decades or even centuries to recover (Duffy and Meier, 1992; Matlack, 1994), tests for microhabitat preferences should be strongest in old-growth forest.

We have therefore conducted a detailed characterization of the range of micro-environments in which four *Carex* species grow at Mont St. Hilaire. We investigated three species in the upland-species group, *Carex backii* F. Boott., *C. communis* L.H. Bailey, and *C. platyphylla* Carey, to test for microhabitat preferences that were not evident in a broad-scale survey of the study site (Bell, Lechowicz, and Waterway, 2000). We also investigated *C. plantaginea*, to test for environmental correlates of its unique distribution among the *Carex* species at Mont St. Hilaire. Distinct microhabitat preferences among the four species, particularly the three upland species, would indicate that environmental heterogeneity plays an important role in maintaining the diversity of forest-understory *Carex* species. We have also made a preliminary assessment of the relationships between environment and plant characteristics to gain insight into the important factors controlling the distribution of each individual species.

MATERIALS AND METHODS

Study site and species—Mont St. Hilaire (45°32' N, 73°8' W) is a 1200-ha UNESCO Biosphere Reserve located ~35 km east of Montréal, Québec, Canada. The reserve is dominated by sugar maple (*Acer saccharum*) and American beech (*Fagus grandifolia*) and is the largest remaining tract of old-growth deciduous forest in southern Québec. The geology, microclimate, hydrology, vegetation, and natural history of Mont St. Hilaire have been described elsewhere (Maycock, 1961; Rouse and Wilson, 1969; Feininger and Goodacre, 1995).

From among the 50+ *Carex* species occurring on Mont St. Hilaire, the four we chose to study share a caespitose growth form and occur predominantly on upland sites. Leaves of all four species remain green throughout the winter and senesce in spring and summer as new leaves expand (Handel, 1978a; M. Vellend, personal observation). Flowering begins in early spring for *C. plantaginea* and is followed over a period of 3–4 wk by *C. communis*, *C. platyphylla*, and *C. backii*, respectively, all of which overlap considerably in their reproductive schedules. Seeds drop in early summer (June) for *C. plantaginea*, closely followed by *C. communis* and *C. platyphylla*, and finally *C. backii* in early July. Seeds of *C. plantaginea* and *C. platyphylla* are known to be gravity dispersed (Handel, 1978a) and seeds of *C. communis* are at least partly ant-dispersed (Handel, 1978b). In the absence of any specialized structure for

seed dispersal (M. Vellend, personal observation), we assume that *C. backii* is gravity dispersed.

Because sparsely distributed species yield sparse data when study plots are placed randomly within a given habitat (e.g., Hicks, 1980; Crozier and Boerner, 1984), we targeted plots around individuals of each species. Thirty individuals each of *C. backii*, *C. communis*, *C. plantaginea*, and *C. platyphylla* were chosen in 1996 as focal plants, around which circular 1-m² plots were established. We surveyed all of Mont St. Hilaire for areas in which each species occurred, and then chose focal plants randomly within each area with the one restriction that no two plots be <10 m apart. We did not often find the four species in discrete populations, so the 15 areas that we sampled ranged in size from <1 ha to as large as 25–30 ha. Of the original 120 plots, 16 were ruined by vandalism in autumn 1996. Following establishment of additional plots in April 1997, we collected data at 32 *C. backii* plots (including six where *C. communis* or *C. platyphylla* also grew), 28 *C. communis* plots, 28 *C. plantaginea* plots (one of which contained *C. communis*), and 29 *C. platyphylla* plots (in six of which *C. backii* or *C. communis* were also found). When referring to environmental characteristics of these four types of plots, we will use the term *plot type*; when referring to plant characteristics, we will use *species*.

Monitoring of micro-environments—We measured a set of environmental variables during the growing season of 1997 to assess as completely as possible the range of factors that may influence species' distributions. Aspects of availability of all resources potentially limiting to plants, water, light, and mineral nutrients, were measured. To yield quantitative descriptors of forest composition and maturity around each plot, we identified to species and measured the diameter at breast height (DBH) of all tree stems >10 cm DBH in a 100-m² circle around each focal plot. We also recorded the percentage cover of each vascular plant species in each 1-m² plot within five cover classes (Braun-Blanquet, 1965). Slope angle was measured with a clinometer between two points: 2–3 m upslope and 2–3 m downslope from each plot.

We estimated the percentage of ambient light reaching the forest floor (non-interceptance of diffuse radiation) using two LAI-2000 Plant Canopy Analyzers (LI-COR Environmental Division, Lincoln, Nebraska, USA; Welles and Cohen, 1996). One instrument was left under open sky at the base station on Mont St. Hilaire; the other was carried from plot to plot in the forest. Estimates of diffuse noninterceptance (DIFN) were calculated based on a comparison of open-sky and below-canopy readings at equivalent times of day (± 7 sec). Separate readings were taken for the western and eastern halves of the sky on clear days using 50% view restrictors to block direct sunlight (LI-COR, 1992). The mean of western and eastern DIFN estimates at each plot was used as a measure of light availability.

We estimated the percentage cover of leaf litter and bare rock to the nearest 5% within each focal plot. Soil depth was estimated from eight measurements taken with a 50-cm soil probe at random positions within each plot. Because some of the individual depth measurements were >50 cm, we used the median of the eight replicates as a value for each plot instead of the mean. Volumetric soil-water content was estimated from two samples taken on 10 July and 8 October, each sample consisting of four to five soil cores taken to a depth of 7 cm. This depth was chosen because *Carex* roots are concentrated in the top 5–10 cm of the soil horizon (M. Vellend, personal observation). We estimated pH, organic matter content, and exchangeable nutrient content of the 10 July soil sample after air drying and passing through a 2-mm mesh sieve. Soil pH was determined on a 1:2 soil and water suspension (Kalra, 1995), and percentage organic matter content per dry mass of soil was estimated as the percentage mass loss on ignition at 800°C (Ball, 1964). For surface soils at Mont St. Hilaire, a small portion (~2%) of mass loss on ignition may be due to loss of structural water and carbonates (T. R. Moore, McGill University, personal communication); therefore, our values of percentage organic matter may be slightly overestimated (Nelson and Sommers, 1982).

We employed two different methods to estimate soil nutrient availabilities in each plot: ion-exchange resin capsules (Skogley, 1992) and standard chemical extractions of exchangeable nutrients in soil samples (Binkley and Vitousek, 1989). Both analyses were carried out by the University of Alberta

Soil Chemistry Laboratory. Resin-capsule analyses were conducted for the three major macronutrients potentially limiting to plant growth: nitrogen, phosphorus, and potassium (Chapin, 1980). For these nutrients, we report only the resin-capsule results because they are thought to better reflect variation among sites in plant-available nutrients than point-in-time soil samples (Binkley and Vitousek, 1989; Skogley, 1992); differences between the two data sets did not influence our interpretations of important controls on species' distributions (Vellend, 1999). Between 27 and 29 April, two 1-cm diameter mesh spheres filled with a mixed-bed ion-exchange resin (resin capsules; UNIBEST Inc., Bozeman, Montana, USA) were buried at 7 cm depth at random positions on the perimeter of each plot. We retrieved one of the two capsules at each plot on 4 July, the other on 16 September 1997. Nutrient ions were recovered from each capsule in 2 mol/L HCl following method number 20 in Skogley et al. (1997). Exchangeable calcium and magnesium were determined from an NH_4 OAc extract of soil samples at pH 7 (Chapman, 1965).

Monitoring of characteristics of focal plants—During the first year of study, 1996, we counted all shoots, both vegetative and flowering, on all plants of the focal species in each plot; these 1996 data were used to quantify the density, abundance, and average plant size of the focal species in each plot. Over the next two years, 1997 and 1998, we counted vegetative and flowering shoots only on the focal plant in each plot; we used these data to calculate measures of reproductive allocation and relative growth for individual plants. Other than the shoot counts, all measurements on plants were taken in 1997.

We estimated the chlorophyll content per unit leaf area of each focal plant with a SPAD-502 Chlorophyll Meter (Minolta Camera Company, Ltd., Tokyo, Japan) on two occasions, 10 June and 5 August. On each occasion we took 16 SPAD readings on randomly chosen leaves of each focal plant. On a sample of seven to ten leaves of each species from outside the focal plots we took SPAD readings as above and measured leaf chlorophyll concentration in dimethyl sulfoxide extracts (Spencer and Ksander, 1987) to develop a quadratic regression model predicting leaf chlorophyll content from the SPAD measurements ($r^2 = 0.96$; Vellend, 1999). We used the mean of all 32 SPAD readings for each focal plant to yield one estimate of chlorophyll content.

On 27 July we collected four small discs of leaf tissue from the center of randomly chosen leaves on each focal plant. Leaf samples were dried for 72 h at 70°C and weighed to the nearest 0.1 mg to determine specific leaf area (SLA). We estimated the nitrogen content of each set of four leaf discs in an EA 1108 CHNS-O elemental analyzer (Fison Instruments, Milan, Italy).

Statistical analyses—To determine the degree to which the four species co-occur at Mont St. Hilaire, we used data from Bell, Lechowicz, and Waterway (2000) who surveyed for the presence or absence of all *Carex* species at Mont St. Hilaire in 13 500 4-m² quadrats. We tested the independence of species occurrences using Fisher's exact tests.

The goals of our statistical analyses of environmental data were to describe variation across all plots, and to test for differences among the four plot types for a large number of variables. We treated the plots where more than one of the four species occurred as belonging to the plot type to which it was originally assigned. Discarding the plots with more than one of the four species would introduce a bias into the analyses by not including zones of co-occurrence. All statistical analyses were performed using SAS Version 6.12 (SAS Institute, Cary, North Carolina, USA), unless otherwise indicated.

Three variables derived from the vegetation data were treated as environmental variables. The importance value of each tree species around each focal plot was calculated as the percentage of total DBH plus the percentage of the total number of stems >10 cm DBH accounted for by a given species in a 100-m² circle around each focal plot. Using PC-ORD (McCune and Mefford, 1997), we conducted a detrended correspondence analysis (DCA) of the tree importance values around each plot (Vellend, 1999), and used axis 1 as a variable representing a gradient of forest cover type, ranging from xeric to mesic. The total number of tree stems >10 cm DBH around each plot was considered as a successional axis, with more, smaller tree stems occurring in younger stands. The only variable derived from the herbaceous vegetation

data was the number of species per square metre, not including the focal species.

For each environmental variable, we performed a one-way analysis of variance to test for differences among plot types. Variables were transformed where necessary to improve normality for parametric analyses (see Results). In cases where the assumption of normality could not be met, data were transformed to ranks and analyzed in a nonparametric one-way Kruskal-Wallis test. We performed multiple-comparison tests after each ANOVA on all pairs of plot types using Ryan's Q following parametric ANOVAs and joint-rank Ryan's following nonparametric ANOVAs (Day and Quinn, 1989).

We conducted two different multivariate analyses for two different purposes: (1) to describe environmental variation across all plots and (2) to describe environmental variation among plot types. To summarize the main variation in environmental characteristics across all plots, we conducted a principal components analysis on the whole set of 17 variables. To summarize the main variation in environmental characteristics among plot types we conducted a canonical discriminant analysis (Gittins, 1985) using the four plot types as categories. Canonical discriminant analysis is a multivariate technique that determines the linear combination of input variables that maximizes the ratio of variance among groups (in our case, plot types) to variance within groups (Gittins, 1985). This algorithm is repeated $N-1$ times, where N is the number of groups, each time with the restriction that each axis be uncorrelated with all previous axes.

In addition to our data on leaf chlorophyll concentration, specific leaf area, and nitrogen content, we derived five variables from our data on shoot counts to assess shoot density, species abundance, average plant size, growth rate, and reproductive allocation. Data for the first three variables were taken only in 1996. The five variables are: (1) total number of shoots, vegetative or flowering, per square metre, (2) total number of genets per square metre, (3) mean number of shoots per genet, (4) relative growth rate (RGR) of the focal plant from 1996 to 1998, and (5) mean proportion of shoots that were flowering over 3 yr. RGR was calculated as the difference between the logarithms of the number of vegetative shoots in 1996 and 1998 divided by two. For each variable characterizing the focal plants we conducted a one-way ANOVA among species, with multiple comparisons performed as described above.

For each species separately, we performed a wide range of univariate and multivariate analyses to explore relationships of focal-plant characteristics with environment. As the multivariate analyses yielded no clear and strong patterns within species, we report only selected bivariate relationships that were of interest because of other emerging patterns in the data.

RESULTS

Associations among species—*Carex backii*, *C. communis*, and *C. platyphylla* were found in the same 4-m² quadrats far more often than would be expected if species occurrences were independent of one another (Table 1). The occurrence of *C. plantaginea* among the 4-m² quadrats was statistically independent of the occurrences of each of the other three species.

Univariate environmental differences among plot types—Plot types differed significantly ($P < 0.05$) for all environmental variables except ammonium, potassium, and magnesium (Table 2). However, for soil moisture, nitrate, and pH, significant differences among plot types were due only to *C. plantaginea* plots occurring at the extreme high ends of these gradients. Multiple comparison tests showed all pairs of plot types to be significantly different from one another for two variables: slope angle and forest composition ($P < 0.05$). From xeric to mesic, the order of species on the forest composition gradient was: *C. backii*, *C. platyphylla*, *C. communis*, and *C. plantaginea*.

Variation in environmental variables across all plots—Axes 1–3 of the principal components analysis (PCA) account-

TABLE 1. Fisher's exact test (two-tailed) for patterns of association among four sedge species in 13 500 quadrats (4 m²) surveyed by Bell, Lechowicz and Waterway (2000) at Mont St. Hilaire, Québec. The four species are *Carex backii* (BAC), *C. communis* (COM), *C. plantaginea* (PLA), and *C. platyphylla* (PLY). Each cell contains observed frequency (expected frequency). Significant ($P < 0.05$) associations among species are indicated in boldface.

Species 1	Species 2	Both spp. present	Both spp. absent	Sp. 1 absent and sp.2 present	Sp. 2 absent and sp. 1 present	<i>P</i>
BAC	COM	77 (20)	12 344 (12 287)	878 (935)	201 (258)	1.8 × 10⁻²⁶
BAC	PLY	49 (6)	12 981 (12 938)	241 (284)	229 (272)	4.8 × 10⁻³¹
COM	PLY	92 (21)	12 347 (12 276)	198 (269)	863 (934)	1.1 × 10⁻³⁶
BAC	PLA	2 (1)	13 184 (13 183)	38 (39)	276 (277)	2.0 × 10 ⁻¹
COM	PLA	5 (3)	12 510 (12 508)	35 (37)	950 (952)	2.0 × 10 ⁻¹
PLY	PLA	2 (1)	13 172 (13 171)	38 (39)	288 (289)	2.1 × 10 ⁻¹

ed for 23, 18, and 12% of the variance in the environmental data, respectively (Figs. 1 and 2). *Carex plantaginea* was found in the wettest, most nitrate-rich plots, on the shallowest slopes, with the greatest cover of leaf litter, and in association with tree species most characteristic of mesic habitats (*Acer saccharum* and *Fagus grandifolia*). *Carex backii* and *C. platyphylla* were found with strongly overlapping distributions at the opposite end of this gradient, in relatively dry, nitrate-poor plots, on steep slopes, with low leaf-litter cover. *Carex communis* occupied plots in the broadest range of environmental conditions and overlapped considerably with the other three plot types.

Variation in vegetation across all plots—Detrended correspondence analysis (Jongman, ter Braak, and van Tongeren, 1995) of the herbaceous vegetation data revealed a pattern similar to the PCA described above (Vellend, 1999, figure not shown). *Carex plantaginea* was found in association with the most distinct set of taxa, often occurring with taxa characteristic of wet-mesic habitats such as *Arisaema triphyllum*, *Asarum canadense*, *Athyrium thelypteroides*, *Caulophyllum thalictroides*, and *Impatiens* spp. The herbaceous vegetation at *Carex backii* and *C. platyphylla* plots was broadly similar, though the vegetation at *C. backii* plots was more variable than at *C. platyphylla* plots. These two species were often found with taxa typical of dry-mesic habitats such as *Saxifraga virginensis*, *Dryopteris marginalis*, *Aster macrophyllus*, and *Aralia nudicaulis*. *Carex communis* was found with the largest number of different herbaceous taxa, including several commonly occurring taxa at Mont St. Hilaire, such as *Erythronium americanum*, *Polygonatum pubescens*, *Thalictrum dioicum*, and *Maianthemum canadense*.

Multivariate environmental differences among plot types—Axes 1–3 of the canonical discriminant analysis (CDA) accounted for 63, 28, and 9% of the environmental variation among plot types, respectively, and all three axes had canonical correlations with the plot types that were significantly different from zero ($P < 0.02$). In contrast to the PCA, there was a strong differentiation between *C. backii* and *C. platyphylla* plots on axis 2 of the CDA (Fig. 3). The differences between *C. plantaginea* plots and both *C. platyphylla* and *C. backii* plots were greatest, with lesser differences among the other pairs of plot types. As in the PCA, *C. plantaginea* plots were associated with high levels of soil moisture and available nitrate, shallow slopes, mature mesic tree species, and low levels of soil organic matter (Table 3). Again, *C. backii* and *C. platyphylla* occurred at the opposite end of this gradient from *C. plantaginea*, but were differentiated in the CDA on axis 2

because of shallower slopes, lower pH, more xeric tree species, and higher available phosphorus at *C. backii* plots. *Carex communis* occurred in the broadest range of environmental conditions, overlapping considerably with the other plot types.

Species and focal plant characteristics—Shoot density per plot varied over more than an order of magnitude for each of the four species. Considering all plants observed in all plots, there were distinct differences in the distributions of shoots per genet among species (Fig. 4). *Carex plantaginea*, *C. platyphylla*, and *C. communis* had the most individuals in the smallest size classes, with a decrease towards the larger size classes. Maximum shoot number was distinctly lower for *C. platyphylla* than for the others (Fig. 4). The size distribution of *C. backii* showed relatively few individuals of small size, with a median shoot number (nine) at least three times higher than the medians of the other three species, when all individuals in all plots were considered. The mean relative growth rate between 1996 and 1998 was positive for all four species, but RGR was significantly different from zero only for *C. communis* (two-tailed *t* test, $P < 0.01$).

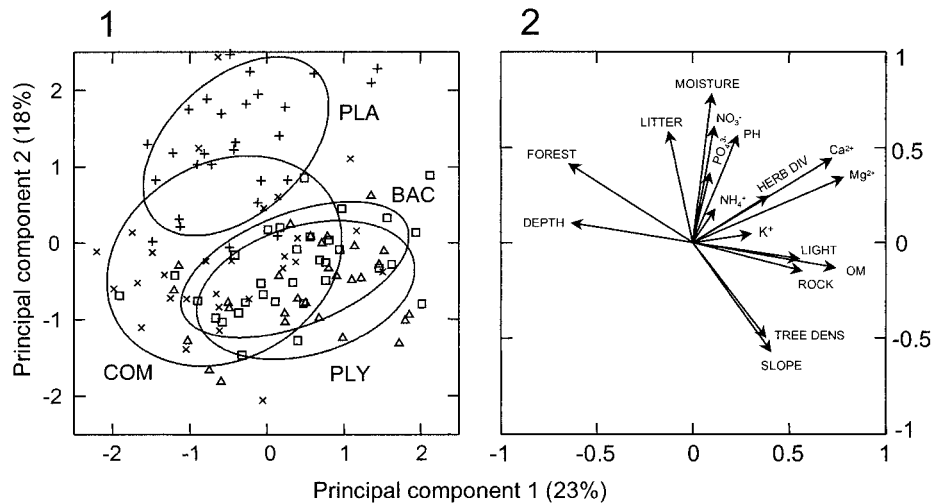
All variables characterizing the focal plants, except RGR, varied significantly among species ($P < 0.05$, Table 4). The two wide-leaved species, *C. plantaginea* and *C. platyphylla*, had fewer shoots per genet, and more genets per square metre than the two narrow-leaved species, *C. backii* and *C. communis*. *Carex plantaginea*, the species found in the sites with the highest nitrate availability, had the highest percentage leaf nitrogen. Leaf chlorophyll content per area was highest in the two species from the most xeric environments, *C. backii* and *C. platyphylla*. *Carex backii* was also the species occurring in plots with the highest light availability (Table 2) and had the lowest specific leaf area (Table 4).

DISCUSSION

Environmental heterogeneity and interspecific differences in microhabitat preferences appear to be important factors contributing to the maintenance of species diversity within the genus *Carex* in the forest understory. Both phytosociological studies in our region (Walther, 1963; Op de Beeck, 1972) and ongoing investigations at Mont St. Hilaire indicated that the environmental distribution of *C. plantaginea* was distinct from the other three species. This expectation was confirmed in all of our analyses (Table 2, Figs. 1 and 3). In northeastern North America, *C. backii*, *C. communis*, and *C. platyphylla* all occur in mesic to dry-mesic deciduous forest habitats (Curtis, 1959; Maycock, 1961; Walther, 1963; Op de Beeck, 1972; Gagnon and Bouchard, 1981), and frequently co-occur at Mont St. Hi-

TABLE 2. Environmental characteristics at 1-m² focal plots of *Carex backii* (BAC), *C. communis* (COM), *C. plantaginea* (PLA), and *C. platyphylla* (PLY) with analyses of variance among plot types for each variable. All ANOVAs are parametric with the exception of those based on ranked data, which are equivalent to Kruskal-Wallis tests. For a given variable, different superscript letters indicate significant differences ($P < 0.05$, Ryan's Q procedure for parametric tests, joint-rank Ryan's for nonparametric tests). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Variable	Units	Mean (median) ± 1 SD					Transformation for analysis	F
		BAC	COM	PLA	PLY			
FOREST	standardized ordination units: low values xeric, high values mesic.	-0.84 ^a (-1) ± 0.72	0.36 ^c (0.55) ± 0.92	0.84 ^d (0.61) ± 0.59	-0.23 ^b (-0.51) ± 0.85	none	25.8***	
TREE DENS	no. tree stems > 10 cm DBH / 100 m ²	7.1 ^c (7) ± 2.4	5.6 ^b (5) ± 2.8	3.3 ^a (3) ± 1.8	6.2 ^{b,c} (6) ± 2.1	none	14.2***	
HERB DIV	no. herbaceous species / m ²	6.8 ^{ab} (6.5) ± 1.5	6.3 ^a (6) ± 2.5	7.9 ^{b,c} (7.5) ± 2.3	8.6 ^c (9) ± 2.8	none	5.9***	
SLOPE	degrees from horizontal	26.7 ^c (28.5) ± 8.3	19.8 ^b (21) ± 9.4	12.7 ^a (12) ± 10.7	35.5 ^d (38) ± 8.5	none	31.6***	
LIGHT	% diffuse noninterception	2.9 ^b (2.6) ± 1.3	1.9 ^a (1.7) ± 0.8	2.1 ^{ab} (1.6) ± 1.5	2.5 ^{ab} (2) ± 1.4	arcsin-sqrt	3.9***	
LITTER	% cover of leaf litter	55 ^b (65) ± 26	52 ^{ab} (50) ± 24	75 ^c (80) ± 18	38 ^a (35) ± 21	arcsin-sqrt	12.6***	
ROCK	% cover of bare rock	9.7 ^{ab} (5) ± 11.2	5.5 ^a (0) ± 11.4	6.8 ^{ab} (2) ± 13.2	17.1 ^b (10) ± 18.9	rank	6.3***	
DEPTH	cm	22.7 ^{ab} (18) ± 15.2	29.5 ^b (27.5) ± 15.7	28.5 ^{ab} (28.5) ± 15.9	17.8 ^a (14.5) ± 11.1	rank	4.1**	
OM	% organic matter of soil dry mass	18.7 ^b (24.2) ± 15.5	24.2 ^{ab} (20.6) ± 13.1	17.0 ^a (16.9) ± 6.8	30.6 ^b (29.1) ± 13.1	ln	6.8***	
MOISTURE	% H ₂ O of soil volume	19.9 ^a (20.1) ± 4.7	20.7 ^a (19.6) ± 6.1	30.7 ^b (27.6) ± 11.4	18.2 ^a (18.4) ± 4.0	ln	18.1***	
PH	-log [H ⁺]	5.0 ^a (4.9) ± 0.5	4.9 ^a (4.9) ± 0.5	5.7 ^b (5.7) ± 0.5	5.2 ^a (5.2) ± 0.4	none	12.8***	
AVAIL NO ₃ ⁻	μmol (NO ₃ ⁻) / cm ² (resin capsule surface)	2.3 ^a (0.8) ± 4.5	1.6 ^a (0.9) ± 2	5.3 ^b (2.3) ± 8.1	1.2 ^a (0.8) ± 1.2	ln	5.9***	
AVAIL NH ₄ ⁺	μmol (NH ₄ ⁺) / cm ² (resin capsule surface)	0.5 (0.2) ± 0.8	0.4 (0.2) ± 0.7	0.4 (0.1) ± 0.8	0.3 (0.2) ± 0.3	ln	0.3	
AVAIL PO ₄ ³⁻	μmol (PO ₄ ³⁻) / cm ² (resin capsule surface)	0.26 ^b (0.13) ± 0.45	0.10 ^a (0.05) ± 0.18	0.17 ^{ab} (0.09) ± 0.28	0.09 ^a (0.04) ± 0.2	ln	6.7***	
AVAIL K ⁺	μmol(K ⁺) / cm ² (resin capsule surface)	2.9 (1.6) ± 2.8	2.1 (1.1) ± 2.6	2.0 (1.6) ± 1.7	3.4 (2.2) ± 3.8	ln	1.8	
EXCHG Ca ²⁺	μg(Ca ²⁺) / g (dry soil)	49.4 ^{ab} (362) ± 443	325 ^a (236) ± 289	572 ^b (425) ± 423	513 ^{ab} (437) ± 407	ln	3.2*	
EXCHG Mg ²⁺	μg(Mg ²⁺) / g (dry soil)	34.1 (23.9) ± 25	22.4 (20.3) ± 16.3	27.7 (25.2) ± 13.7	32.8 (31.4) ± 21.8	ln	2.2	



Figs. 1–2. Principal components analysis of 17 environmental variables across 117 1-m² plots at Mont St. Hilaire, Quebec. **1.** Scores for each plot on the first two axes; plot scores on each axis were standardized to a mean of zero and a variance of one. Gaussian confidence ellipses (95%) are drawn for each plot type. □ = *Carex backii*, × = *C. communis*, + = *C. plantaginea*, Δ = *C. platyphylla*. **2.** Factor pattern; the co-ordinate of the tip of a given arrow on a given axis is the Pearson correlation coefficient of the variable with that axis and is thus on a different scale than the plot scores. The longer an arrow, the stronger the effect of that variable in locating plots within the ordination. Abbreviations of variables correspond to those in Table 2.

Figure Abbreviations: BAC, *C. backii*; COM, *C. communis*; PLA, *C. plantaginea*; PLY, *C. platyphylla*;

laire (Table 1). Despite this, we have shown that these three species differ considerably in their small-scale environmental distributions.

Though microhabitat preferences of forest herbs have been demonstrated previously, the choice of species makes this study an important contribution to our understanding of forest-herb distribution. Most ecological studies on the distribution of forest herbs have been of two general types. Synecological studies have generally focused on the more common species at a given study site, often resulting in a classification of spe-

cies into groups based on environmental correlates of habitat distribution (e.g., Bratton, 1976a; Hicks, 1980; Graves and Monk, 1982; Menges and Waller, 1983; Beatty and Sholes, 1988). Autecological studies generally emphasize the importance of one or a few resource gradients for the distribution and performance of individual species (e.g., Pitelka, Ashmun, and Brown, 1985; Lechowicz, Schoen, and Bell, 1988; Marino, Eisenberg, and Cornell, 1997). In contrast, we investigated a group of functionally similar congeners that are all relatively infrequent compared to the dominant herbs in the forest understory. Our results suggest that environmental heterogeneity is an important determinant of interspecific distribution patterns in the forest understory not just for common species (Bratton, 1976b; Crozier and Boerner, 1984; Beatty, 1985), but

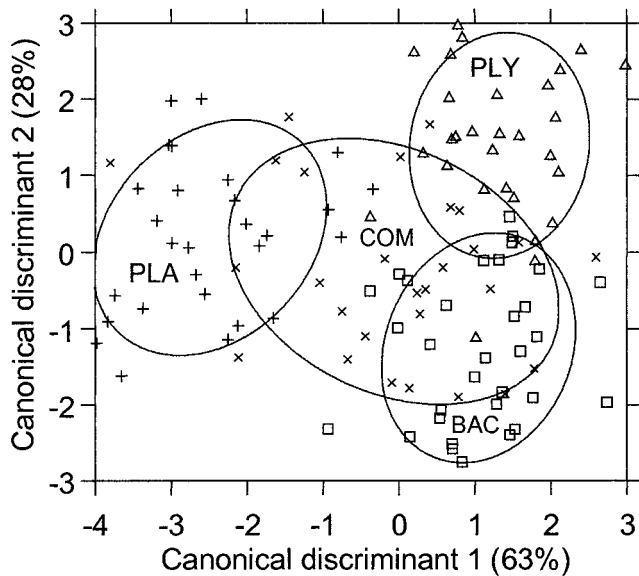


Fig. 3. Canonical discriminant analysis of 17 environmental variables among four plot types at Mont St. Hilaire, Quebec. Abbreviations of variables correspond to those in Table 2. Gaussian confidence ellipses (95%) are drawn for each plot type. □ = *Carex backii*, × = *C. communis*, + = *C. plantaginea*, Δ = *C. platyphylla*. See Table 3 for standardized canonical coefficients.

TABLE 3. Standardized canonical coefficients on two axes from a canonical discriminant analysis based on 17 environmental variables among four plot types. See Fig. 3 for the distribution of plot types on the two axes. Abbreviations correspond to those in Table 2.

Variable	Axis 1	Axis 2
OM	0.48	0.38
SLOPE	0.47	0.74
TREE DENS	0.34	-0.03
AVAIL PO ₄ ³⁻	0.29	-0.68
HERB DIV	0.12	0.50
ROCK	0.11	0.12
AVAIL K ⁺	0.07	0.35
LIGHT	0.04	-0.15
DEPTH	0.04	-0.17
AVAIL NH ₄ ⁺ N	-0.02	0.06
EXCHG Mg ²⁺	-0.03	-0.29
EXCHG Ca ²⁺	-0.18	-0.20
PH	-0.28	0.69
FOREST	-0.28	0.92
LITTER	-0.31	-0.17
AVAIL NO ₃ ⁻ N	-0.34	0.18
MOISTURE	-0.49	-0.10

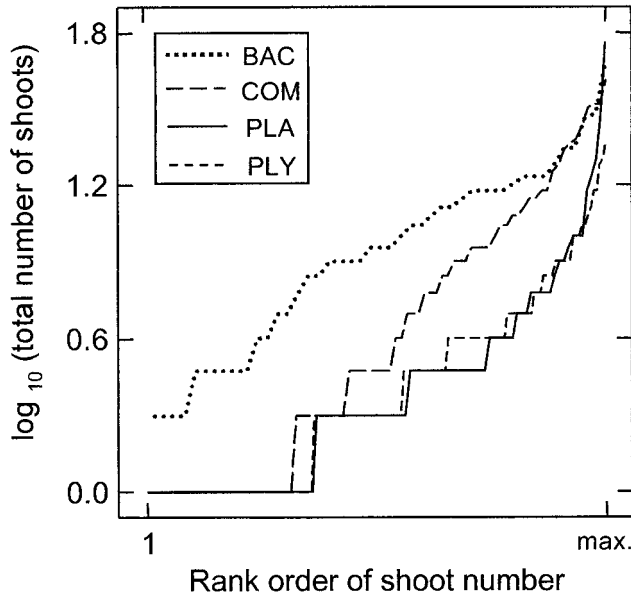


Fig. 4. Quantile plots showing the shoot-per-genet distribution of individuals of four *Carex* species at Mont St. Hilaire, Québec: *Carex backii*, $N = 45$; *C. communis*, $N = 79$; *C. plantaginea*, $N = 99$; and *C. platyphylla*, $N = 155$.

also for relatively infrequent species within a functional group (upland *Carex* species).

According to Grubb's (1977) ideas about the components of a plant species' niche, we have established differences in the "habitat niche" among the four species. This result suggests that current environmental conditions exert control over species distributions, either directly, by their interaction with species' physiological tolerance limits, or indirectly, via biotic constraints that vary along environmental gradients. Such an interpretation is consistent with community theories that assume local variation in community composition is in equilibrium with resource gradients (Tilman, 1982). However, to the degree that species distributions are determined by historical factors, such as dispersal events or disturbance regime, community composition will not be in equilibrium with current environmental gradients (Palmer, 1994). Distribution patterns may, of course, result from a variety of interacting factors, though some factors may dominate at different scales of observation. To evaluate the degree to which the distribution of each of the four species is in equilibrium with current environmental variation among microsites at Mont St. Hilaire, we carefully considered the data on plant characteristics and environment, knowledge of historical disturbance regime, and all available information in the literature. The following paragraphs summarize the salient points from the evaluation of each species.

Carex plantaginea occurred in plots at the wet end of a moisture gradient in our study (Table 2, Figs. 1 and 2), often growing in association with other herbaceous species typical of wet-mesic habitats. However, an extensive survey of *Carex* distribution at Mont St. Hilaire (Bell, Lechowicz, and Waterway, 2000) showed that *C. plantaginea* is associated neither with *Carex* species typical of forest seeps (e.g., *C. scabrata* and *C. gynandra*), nor species typical of upland habitats (e.g., *C. backii*, *C. communis*, and *C. platyphylla*). This is because *C. plantaginea* often occurs along the edges of small creeks

TABLE 4. Characteristics of focal plants at 1-m² plots of *Carex backii* (BAC), *C. communis* (COM), *C. plantaginea* (PLA), and *C. platyphylla* (PLY) with analyses of variance among plot types for each variable. All ANOVAs are parametric with the exception of those based on ranked data, which are equivalent to Kruskal-Wallis test. For a given variable, different superscript letters indicate significant differences ($P < 0.05$, Ryan's Q procedure for parametric tests, joint-rank Ryan's for nonparametric tests). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Variable	Units	Mean (median) \pm 1 SD				Transformation for analysis		F
		BAC	COM	PLA	PLY			
SHOOTS	number of shoots / m ²	20.7 ^b (16.5) \pm 17.7	21.5 ^b (18) \pm 12.6	12.9 ^a (9) \pm 12.1	18.3 ^b (12.5) \pm 16.3	ln	ln	5.6**
GENETS	number of genets / m ²	1.6 ^a (1) \pm 0.8	2.9 ^a (2) \pm 4.3	3.2 ^{ab} (2) \pm 3	5.2 ^b (4) \pm 4.4	rank	rank	12.3***
SHOOT/GENET	mean number of shoots per genet	13.8 ^b (9.7) \pm 13.6	13.0 ^b (10) \pm 10.6	6.8 ^a (3) \pm 11.4	4.1 ^a (3.4) \pm 2.7	ln	ln	16.8***
RGR	vegetative shoots (vegetative shoot) ⁻¹ (year) ⁻¹	0.01 (0.05) \pm 0.25	0.17 (0.18) \pm 0.28	0.09 (0) \pm 0.24	0.01 (0) \pm 0.28	none	none	2.0
RA	proportion of total shoots flowering	0.75 ^c (0.79) \pm 0.2	0.27 ^a (0.28) \pm 0.14	0.36 ^a (0.39) \pm 0.22	0.55 ^b (0.6) \pm 0.2	none	none	36.2***
LEAF N	leaf nitrogen content, % of dry mass	2.29 ^a (2.26) \pm 0.57	2.46 ^a (2.23) \pm 0.66	3.10 ^a (2.91) \pm 0.86	2.72 ^{ab} (2.72) \pm 0.66	none	none	7.3***
CHL	mg (chlorophyll) / m ² (leaf area)	188 ^b (190) \pm 17	167 ^a (166) \pm 19	170 ^a (170) \pm 19	197 ^b (195) \pm 23	none	none	14.8***
SLA	m ² (leaf area) / kg (leaf dry mass)	26.7 ^a (25.1) \pm 5.2	41.4 ^b (40.3) \pm 9.2	39.6 ^b (38) \pm 10.2	39.6 ^b (39.6) \pm 6.9	none	none	21.6***

at Mont St. Hilaire (M. Vellend, personal observation). Many of these areas become inundated in spring, but do not remain wet enough throughout the summer months to support wetland *Carex* species.

We suggest that the distribution of *C. plantaginea* is determined primarily by its requirements for high soil moisture and perhaps nitrogen and its inability to tolerate drier conditions on poor soils and on steeper, more exposed slopes. *Carex plantaginea* had the highest percentage leaf nitrogen of the four species (Table 4), and there was a significant positive correlation between soil nitrate availability and leaf nitrogen ($P < 0.02$). Our data also showed that both total shoot number and reproductive allocation of the focal *C. plantaginea* plants were positively correlated with nitrate availability; reproductive allocation was also correlated with soil moisture. Handel (1976a) investigated the distribution of *C. plantaginea* and *C. platyphylla* on a ravine slope in deciduous forest near Ithaca, New York. As in this study, the two species were found at opposite ends of a moisture gradient, and Handel (1976a) showed that *C. plantaginea* was restricted to the lower part of the slope because of excessive water stress and desiccation on the upper part of the slope. The local distribution of *C. plantaginea* in at least two localities appears to be in equilibrium with current environmental conditions.

At Mont St. Hilaire, *C. platyphylla* is restricted to steep slopes with low leaf litter cover and shallow, dry, and rocky soils with high organic matter content and low nitrogen and phosphorus availabilities (Figs. 1 and 2). However, reproductive allocation and shoot density for *C. platyphylla* were positively related to soil depth, and focal plant size was positively correlated with nitrate availability. These results suggest that *C. platyphylla* may be restricted to poor soils on steep slopes due to a biotic limitation. In his study of *C. plantaginea* and *C. platyphylla*, Handel (1976a) showed that *C. platyphylla* was restricted to the upper part of the slope at his study site due to slug herbivory on the lower part of the slope. However, at Mont St. Hilaire, no evidence of damage by herbivores on *C. platyphylla* plants transplanted to *C. plantaginea* plots was observed (Vellend, 1999). The distribution of *C. platyphylla* may be limited by another biotic factor at Mont St. Hilaire, such as low competitive ability at rich sites. Though the local distribution of *C. platyphylla* may be proximately limited by biotic factors, these limitations appear to be in equilibrium with current environmental gradients. The equilibrium interpretation of the distributions of *C. plantaginea* and *C. platyphylla* is particularly interesting in that *C. plantaginea* and *C. platyphylla* are classified in the same section of *Carex* (*Carex anae*), suggesting a possible evolutionary niche differentiation between these two closely related species.

Dispersal capacity may be an important determinant of the distribution and abundance of *C. communis*. *Carex communis* is the most frequently encountered caespitose *Carex* species at Mont St. Hilaire (Bell, Lechowicz, and Waterway, 2000) and occurred in the broadest range of environmental conditions in this study (Figs. 1 and 2). It is also the only one of the four studied species to be dispersed by ants (Handel, 1978b), and the only one whose seeds will germinate without overwintering or stratification (Bond, 1999). In addition to *C. plantaginea* and *C. platyphylla*, Handel (1976b, 1978a) investigated the distribution and dispersal ecology of *Carex pedunculata*, another ant-dispersed species, and concluded that the evolution of ant dispersal may be explained by the increased probability of reaching unoccupied microsites where *C. pedunculata* could

establish in the relative absence of competition. Kjellsson (1985) came to a similar conclusion for a European ant-dispersed species, *C. pilulifera*. Handel (1978a) labelled *C. pedunculata* a "fugitive" species, because it has greater dispersal capacity, more rapid germination, and faster growth in the absence of competition than its sympatric congeners. In this study, *C. communis* was the only one of the four species to have a relative growth rate over two years that was significantly greater than zero, and it occurred in plots with the fewest other herbaceous species (Table 2, Figs. 1 and 2). These results suggest that *C. communis* may also benefit from ant dispersal due to an increased probability of colonizing microsites where competition is relatively weak and it can grow rapidly. In a companion paper (Vellend, Lechowicz, and Waterway, 2000), we report an experimental test of dispersal limitation in *C. communis* and expand on the evaluation of Handel's hypothesis.

Past disturbance events are likely to be important determinants of the distribution of *C. backii* at Mont St. Hilaire. Along with *C. platyphylla*, *C. backii* occurred at the dry end of a moisture gradient (Figs. 1 and 2). However, *C. backii* plots had higher phosphorus availability, lower pH, and significantly different tree species composition than *C. platyphylla* plots (Tables 2 and 3, Fig. 3). Around *C. backii* plots, the canopy trees differed from those around the other plot types in that they typically included many relatively small individuals of *Quercus rubra* (northern red oak). The size distribution of *C. backii* individuals differed markedly from the other three species, with very few individuals of small size (Fig. 4), suggesting that *C. backii* may therefore occur in "remnant" populations (sensu Eriksson, 1996) at Mont St. Hilaire with little current recruitment under closed canopy. Of the eight peaks at Mont St. Hilaire, *C. backii* is most abundant on Burned Hill, which experienced a major fire in 1948. Fourteen of the 32 *C. backii* plots were on Burned Hill, with five more on an adjacent peak, Sugar Loaf, where fires also occurred in the 1940s. Four more *C. backii* plots were on the northwestern flanks of Dieppe peak, where a major fire occurred in 1957. Smaller ground fires burn on Mont St. Hilaire every few years, though their exact locations have not been documented. We suggest that the environmental distribution of *C. backii* differs from the other three species at Mont St. Hilaire due to long-term effects of past disturbance events like fire on local environmental conditions. Several other *Carex* species have been shown to increase in abundance following fire (Scheiner and Teeri, 1981; Mallik, Hobbs, and Legg, 1984). A high stem density of small oak trees and relatively high light availability indicate that *C. backii* occurs in stands that are in earlier stages of succession compared to the other three species. High soil phosphorus at *C. backii* plots may represent a long-term residual effect of increased nutrient input to the soil from the ash layer and retention of relatively immobile phosphates after fire (Debano, Neary and Ffolliott, 1998). *Carex backii* plots on Burned Hill, Dieppe Peak, and Sugar Loaf had higher phosphorus availability than *C. backii* plots elsewhere on the mountain. Furthermore, there were no correlations between phosphorus availability and any of the variables characterizing the focal plants, suggesting that there is no direct effect of phosphorus gradients on the distribution of *C. backii*.

In summary, environmental heterogeneity and contrasting microhabitat preferences of each species are important factors in maintaining the diversity of forest-understorey *Carex* species. The distributions of *C. plantaginea* and *C. platyphylla*

appear to be in equilibrium with current environmental conditions. However, the distributions of *C. backii* and *C. communis* may be dependent on disturbance and colonization events, respectively, to some degree uncoupled from currently observed environmental gradients. Thus, though our focus was on microhabitat preferences, the results indicate that several factors may be important in determining species' distributions and maintenance of diversity within a single system (Huston, 1994; Palmer, 1994). We suggest that there is a need to test mechanistic hypotheses concerning the limits to distribution of co-occurring species. The role of germination and establishment in distinguishing the distributions of these four congeners is addressed in a companion paper (Vellend, Lechowicz, and Waterway, 2000).

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