

Environmental heterogeneity and species diversity of forest sedges

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Summary

1 A field experiment was designed to investigate the relationship between environmental heterogeneity and species diversity in a group of sedges (Cyperaceae: *Carex*) growing in old-growth forest.

2 A measure of environmental quality, as perceived by the sedges, was obtained from the survival of clonal ramets of 11 species of *Carex* planted at 10-m intervals along each of three 1-km transect lines.

3 The resident assemblage of sedges was censused along the same three transect lines and along a further 24 km of survey lines in the same forest.

4 The general state of a site was represented by the overall survival of the experimental implants at that site. The general environmental variance between sites provided a measure of environmental heterogeneity. This could be partitioned into a specific variance (mean environmental variance of species) and an environmental covariance. The rate of increase of the general and specific variances with distance between sites reflected environmental structure.

5 The three transects differed in scale. The species diversity of the resident *Carex* assemblage was correlated with general environmental quality both among and within transects.

6 The three transects differed in structure. The number of resident species, relative to the number expected from the number of individuals sampled, was greatest on the most coarse-grained transect (steepest increase in general environmental variance with distance).

7 Within each transect, species diversity increased with general environmental variance because the specific correlation of performance (correlation among species of survival in pair-wise combinations of sites) decreased as the general environmental variance increased.

8 The effect of specific environmental variance was weaker. Overall survival of a species on the transects was not correlated with its abundance in the forest. Neither the transects nor a targeted implant experiment provided evidence for a close relationship between the distribution of species and the state of the environment.

9 As a general explanation of our results, we propose a 'marginal-specialist' model in which the species that dominate the most productive sites also have the broadest ranges, whereas other species are superior in a more restricted range of less productive sites.

Keywords: abundance, *Carex*, habitat, implant, plasticity, range, stability, transplant

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Introduction

The diversity of ecologically similar organisms that live together has for long been a central issue in community ecology. The best adapted species should long ago have replaced all the others, unless the process of replacement through competition is continually obstructed or interrupted. In a heterogeneous environment where patches offer different conditions for growth, or have been disturbed at different times in the past, competitive exclusion is likely to be very slow, and might never reach completion (Palmer 1994). More heterogeneous environments would then be expected to support a greater number of species (Williams 1964), as many studies have reported (see general reviews by Shmida & Wilson 1985; Auerbach & Shmida 1987; Hart & Horwitz 1991; Cornell & Lawton 1992; Shorrocks & Sevenster 1995).

Species diversity seems to be related to the structural complexity of the environment in many different kinds of system. Early work by MacArthur showed that bird species diversity is related to the vertical heterogeneity of the canopy (MacArthur 1958, 1964; Recher 1969). In a rather similar way, the number of species of soil mites increases with the complexity of the soil profile (Anderson 1978). Insect diversity is related to the structural or architectural diversity of their plant hosts (Murdoch *et al.* 1972; Strong & Levin 1979; Moran 1980), and fish diversity to the structural complexity of aquatic vegetation (Tonn & Magnuson 1982). The number of species of lizard is related to the complexity of the physical environment in desert communities (Pianka 1967). The diversity of the macrobiota, although not the microbiota, of the rocky intertidal is greater at structurally complex sites provided by seaweed holdfasts or clumps of barnacles than on bare rock (Thompson *et al.* 1996). Structural diversity provided by physical or biotic features is associated with greater diversity of several groups of benthic marine organisms, including microbiota (Pringle 1990), invertebrates (Hewatt 1935) and snails (Kohn 1967). The number of species of freshwater snails also increases with the variety of substrates available (Harman 1972). The number of bird species increases with number of distinct habitats independently of area in islands of a Finnish archipelago (Haila 1983; Haila *et al.* 1983). The number of species of mammals is greater in western districts of North America, which are topographically more heterogeneous than central and eastern districts (Kerr & Packer 1997). Plant species diversity in the Appalachians increases with the number of distinct communities and the number of mountain peaks in the survey area, suggesting a similar link with topographic and ecological heterogeneity (White & Miller 1988). There is also a certain amount of experimental evidence for the theory. For

example, Vivian-Smith (1997) manipulated microtopography in experimental plots and found that hummock-hollow sites supported more diverse plant assemblages than flat surfaces (Silvertown & Wilkin 1983). The relationship between diversity and the heterogeneity created by disturbance has been reviewed at length by Huston (1994).

Not all results are consistent with this view. For example, Nilsson *et al.* (1988) found no relationship between species diversity and the number of types of habitat for woody plants, carabid beetles and land snails on islands in a Swedish lake. Moreover, there is a pervasive difficulty concerning the spatial scale at which surveys are conducted. Böhning-Gaese (1997) found that bird species diversity around Lake Constance was correlated with habitat diversity only at sampling scales of between 4 and 36 km², perhaps because such moderate spatial scales correspond with the distances over which the activity or dispersal of the organisms occurs. Less effect of habitat diversity will be seen either at larger scales or at smaller scales where immigration may overwhelm competition. This may be why, in a very careful study of plant communities of 0.1-ha plots in North Carolina forests, Palmer (1991) found that species diversity was related to the mean value of soil nutrients such as magnesium but not to their variance within plots. The appropriate scale for testing the theory must therefore be chosen carefully to be appropriate for the group of organisms being studied.

We aimed to determine the most appropriate measure of environmental heterogeneity, and to evaluate its relationship to species diversity. The simple approach of measuring physical variables such as pH or nitrate concentration (Lechowicz & Bell 1991) has the drawback that patterns of variation in physical factors cannot be translated readily into terms of plant response. Sowing soil cores taken from the forest with genetically uniform material of barley and *Arabidopsis* (Bell & Lechowicz 1991) allows environmental variation to be described in terms of plant response with great precision, but many of the sources of difference among sites are lost by transferring the soil to the glass-house bench. A third technique is to take seedlings of native plants from forest sites, raise them in enclosures, cross them to create seed families of known provenance, and then plant the seeds back into the parental site (Schoen *et al.* 1994). This is satisfactory in principle, although in practice the complications of sexual inheritance and the rapid loss of a large proportion of the seeds or seedlings make it difficult to estimate the state of the environment with great precision. Despite their drawbacks, all three techniques have demonstrated that the forest floor is heterogeneous at a scale of several metres, i.e. that there are appreciable differences

between sites 1–50 m apart. Moreover, the first two techniques have demonstrated that the forest floor is structured, i.e. that the variance among sites increases with separation from 1 to about 50 m. The object of this study was to use a bioassay approach to extend our description of the structure of the forest floor to a scale of 1 km, using the results to address the relationship between environmental heterogeneity and species diversity.

A given region supports a set of ecologically equivalent species (in the sense of Bell 1996; species of the same functional kind, in the sense of Huston 1994), the local species pool. We wished to know what determines the total number of species recorded when samples are taken from several sites within this region, and what causes variation in the number of species among sites. Consider any two sites, from which S_1 and S_2 species, respectively, have been recorded. The number of species occurring in the two sites combined (S_{12}) will be:

$$S_{12} = S_1 + S_2 - S_1 S_2 / N - (N - 1) \text{Cov}(X_{ij}, X_{ik})$$

where N is the number of species in the local pool. The number of species in each site separately, S_1 and S_2 , is an effect of scale. It depends on the number of individuals collected, and it cannot be analysed further unless the sites can be further subdivided. The final term on the right-hand side is the covariance of occurrence at the two sites among species: X_{ij} is the occurrence of the i th species at site j , and X_{ik} its occurrence at the other site, k . We shall call this the specific covariance; it would be equivalent to a genetic covariance if the species were treated as genotypes within a population. A low, or negative, covariance indicates that the composition of the assemblage at one site is poorly correlated, or negatively correlated, with its composition at another. One interpretation of a low specific covariance of occurrence is that conditions of growth differ at the two sites, some species being well-adapted to the first site and colleagues to the second. The covariance can then be used as a measure of environmental heterogeneity in terms of overall plant response. It can be thought of as quantifying the concept of among-site or beta diversity (Whittaker 1970), so that the decay of the covariance with distance measures the 'turnover' of assemblage composition.

There are at least two competing interpretations of how species diversity is maintained in spatially heterogeneous environments, illustrated in the two upper panels of Fig. 1. The x -axis of each diagram represents an environmental gradient of some kind, in this case productivity, so that separation along this axis represents environmental variance. The y -axis represents the performance of a given species. Performance, as used here, is best defined as the rate at which this species increases in frequency in a mix-

ture, but in practice it will usually be defined in terms of the survival, growth or reproduction of isolated plants or pure stands. Although this is often the only practicable approach, it may be inadequate when populations are so dense that individuals of different species compete directly. In the classical 'niche-separation' model (Fig. 1a), each species is specialized for thriving in a restricted range of conditions, so that species differ in their mean location along the environmental axis. The height of its distribution at any given point represents the performance of a species at a given state of the environment, and the state to which the species is best adapted is marked by its peak performance. The variance of each distribution is proportional to the ecological range occupied by the species; species do not differ consistently in range, or at least range is not correlated with peak performance. Environmental heterogeneity thus sustains species diversity through local adaptation to qualitatively different conditions of growth at different sites. In contrast, in the 'rare-generalist' model all species have their peak performance at the same environmental state (high productivity), but differ in variance; peak performance is negatively correlated with variance, so the species that dominate the most productive sites have narrow ranges. The most productive sites are dominated by the most responsive species, which are best able to exploit favourable conditions of growth, whereas other species are more stable, being able to maintain themselves even in unproductive sites. A third hypothesis, the 'marginal-specialist' model, will be discussed later. Recent accounts of ecological specialization and variation in plant assemblages include Sultan *et al.* (1998) and Svenning (1999).

In both cases, the species–sites interaction of performance is supposed to lead to a process of selection that sorts species into the sites to which they are best adapted, and this causes the observed species–sites interaction of occurrence. Both theories predict that species diversity will increase with the area sampled. This will be in part an effect of scale, because the number of individuals encountered will increase with area, and in part an effect of structure, because environmental variance will increase with area. It is possible to distinguish the two; the ingenious analysis of forest plant communities by Palmer & White (1994), for example, showed that about two-thirds of the overall increase in species diversity with area was a pure scale effect, the remainder being attributable to function. Both theories predict a pure effect of structure independently of scale: the combined species diversity of two sites will increase with their distance apart.

Given an objective measure of environmental heterogeneity, we would be able to evaluate its relationship with species diversity. The niche-separation theory requires a high degree of local adaptation,

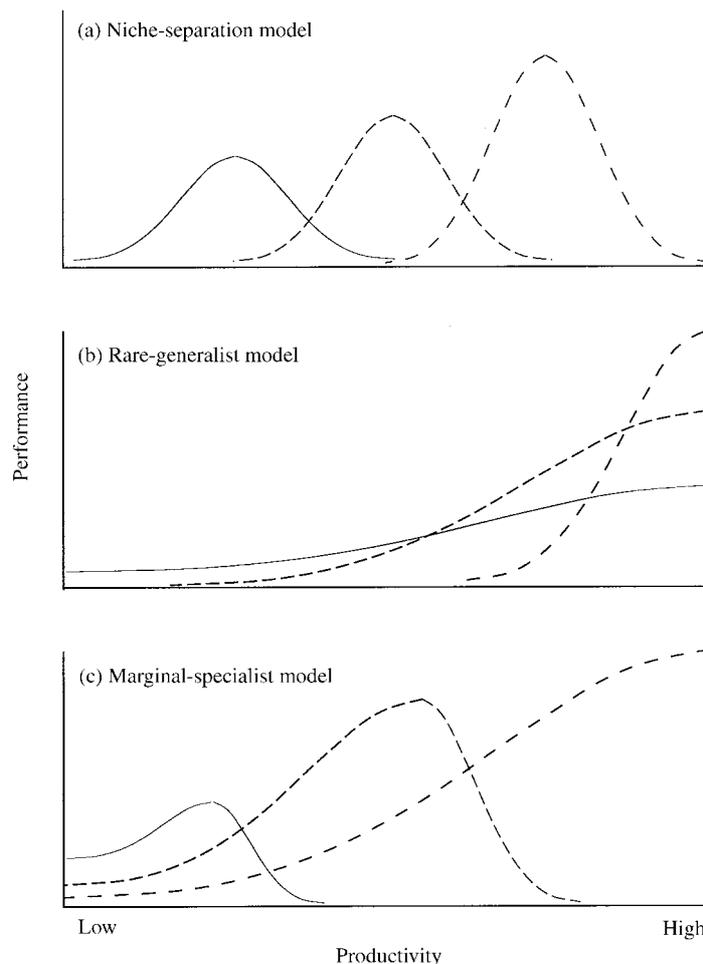


Fig. 1 Three theories of how species are arranged on landscapes. Each curve represents the variation of performance over sites of a given species. (a) Niche-separation model. Each species is specialized to a given range of sites. Mean (or maximal) local abundance of species is uncorrelated with their range (variance). Diversity of sites is uncorrelated with their productivity. (b) Rare-generalist model. Abundance is negatively correlated with range; diversity is positively correlated with productivity. (c) Marginal-specialist model. Abundance is positively correlated with range; diversity is negatively correlated with productivity.

and therefore predicts that the performance of experimental plants at a site will be correlated with the composition of the local assemblage: a species should occur predominantly at sites where its performance is high, and, conversely, its performance should be exceptionally high in the sites where it occurs. Furthermore, the specific covariance should fall with distance, becoming negative at moderate distances. The rare-generalist theory requires only that species respond differently to the general quality of the environment, and local adaptation may be undetectable because many species have broad ranges and are able to survive almost anywhere. The specific covariance will fall with distance, but will remain positive even at large distances.

Materials and methods

STUDY SITE

Our experiments were conducted at the Gault Estate, Mont St Hilaire, Quebec, Canada ($45^{\circ}35'N$, $73^{\circ}9'W$). This is one of the Monteregian hills, isolated basolithic mounts rising about 300 m above the St Lawrence valley floodplain. The hill is covered with a remnant of the deciduous forest of north-eastern North America; with unimportant exceptions, it has never been cut, cultivated or settled, and thus presents a nearly pristine natural environment. The importance of the locality is indicated by its status as a UNESCO Man and the Biosphere Reserve. Further details of the site and its

flora are given by Maycock (1961), Ouellet & LeBlanc (1967) and Holland (1981), and a bibliography of research conducted on the mountain has been published by Levy & Lechowicz (1987).

TRANSECT LINES

We laid out three base ropes, each 1 km in length, in a remote part of the forest where public access was prohibited. Two transects (Gorge and Cliff transects) extended east–west and north–south from a common origin through upland forest. The third (Lake transect) ran through a wetter area alongside the shore of a small lake and formed most of the third side of the triangle. Side ropes 5 m in length were then strung normal to the base rope, and to one side of it, at 10-m intervals. We then used small plastic stakes to define 20 planting positions along each side rope, alternately to right and left of the rope, such that no plot was closer than 50 cm to another. Great care was taken to minimize trampling, and all routine activities were confined to the side of the main rope away from the side ropes.

STUDY SPECIES

Sedges in the genus *Carex* (Cyperaceae) provide exceptionally appropriate material for investigations of diversity. There are more species of *Carex* than of any other genus of seed plants in most forest and wetland habitats in temperate and subarctic regions: of about 2000 species world-wide, about 500 occur in North America and over 50 have been recorded from the 1000-ha of our study site. Furthermore, they can be propagated as genetically uniform clones by vegetative proliferation of material collected in the forest, and the ramets can then be used as biological indicators of the state of the environment at different sites. This provides estimates of environmental heterogeneity as perceived by native plants, which are likely to be superior to those derived from measurements of physical variables because they relate directly to the variation in performance on which both the niche-separation and rare-generalist models are based. They are, however, much more laborious to obtain. We planted ramets of several species of *Carex* at regular intervals along three transects each 1 km in length. The measure of the state of the environment was the survival of these ramets after 12 months.

EXPERIMENTAL PROCEDURES

Several large healthy plants of each of 15 *Carex* species were collected in the forest at Mont St Hilaire and dissociated carefully into ramets, which were then grown individually in potting soil with regular watering and fertilization in a shade house at the

McGill University Field Station at Mont St Hilaire. When large enough, they were again dissociated, and this procedure continued until we had obtained about 120 healthy ramets from a single parental plant; enough, with allowance for loss, to furnish the 100 sites on one of the three transects. The experimental ramets were isolated and grown in $1 \times 1 \times 2.5$ -cm cubes of potting soil in a seed tray until firmly rooted. They were then taken to a transect and one inserted into a single planting position at each of the 10-m sites and marked with a labelled plastic tag. We took pains not to disturb the sites in any way, other than excavating a small hole in the centre of each plot to receive the soil plug bearing the experimental ramet. For logistic reasons, a species was assigned the same position at each site on a given transect; however, positions for a given species were assigned independently on the three transects. Although a total of 15 species was used in these experiments, only 11 were common to all three transects (see the Results). In general, a different clone of each species was planted on each transect, in order to complete the experiments within a reasonable period of time. The exception was an unusually prolific clone of *Carex bromoides*, which supplied enough material to set out two replicate ramets at each site on all three transects. These ramets were used to estimate the repeatability of our scores, and are not included in the analyses of environmental structure, for which other clones of *C. bromoides* were available. Planting was carried out in 1993 and 1994 as material became available, and the plants were scored for survival 12 months later. Although more elaborate measurements are possible, the rapid loss of many of these implants under field conditions reduces their usefulness. The procedure provides information about the response of each species to environmental variation, but in this study we were concerned only with the bulk response of the set of species; the particular response of individual species will be analysed in a subsequent paper. Differences between 1993 and 1994, and between spring (May) and autumn (August) planting dates, would contribute to the variation among species on a given transect, or among transects for a given species, but would not contribute to the variation among sites within a transect.

PHYSICAL FACTORS

Various physical features of the environment were scored at every other site, i.e. at 20-m intervals. Those analysed here were three scalar variables: canopy cover, ground cover and soil pH. Canopy cover vertically above the site was estimated on a 10-point scale in July. At the same time, the fraction of the ground surface covered by dead leaves was estimated, again on a 10-point scale. Soil pH was

measured in the laboratory using the protocol described by Lechowicz & Bell (1991).

CENSUS OF NATIVE SEDGES

We also recorded the occurrence of native *Carex* species along a band 1 m either side of the transect line. Each of the experimental sites, at intervals of 10 m, could then be associated with the local sedge assemblage living in this 2-m wide band within 5 m of the site. We could therefore enumerate the species found growing at any pair of sites and thus evaluate the relationship between species diversity and a species-defined measure of environmental variance derived from the experimental ramets.

We also conducted a broader survey of species diversity and abundance. The estate was divided into 12 1-km² blocks, within each of which we scored two 1-km survey lines. The lines in each block were orientated randomly, subject to the constraints that they shared a common origin (and therefore did not intersect) and did not extend beyond the forest border into agricultural land, steep cliffs or permanent open water. Each of the 24 lines was surveyed as a belt transect by locating and identifying every *Carex* plant within 1 m either side of the centre line; each line thus sampled 2000 m², the total area surveyed being 48 ha. The position of each plant was recorded with a precision of 2 m, so the smallest spatial unit of sampling was 4 m². We did not attempt to estimate the number of individual plants of a given species within this area. The surveys were done in two series in 1994 and 1995 from mid-May to mid-July, when it is easiest to identify *Carex* species. It is impossible to identify very young plants with certainty, and these were recorded simply as 'juvenile *Carex* sp.'. Some closely related taxa had to be lumped in cases where the current status of species is disputed (*Carex pensylvanica*/*lucorum* complex) or obscure (*Carex laxiflora* group and *Carex* Section *Ovales*) and are therefore treated as if they were single species. The real species richness of the flora is therefore likely to be somewhat greater than we report here.

TARGETED IMPLANT EXPERIMENT

A flourishing native plant of each of 10 species, all represented among the 15 cloned species, was found near each of the transect lines. A 1 × 1-m quadrat divided at 20-cm intervals was placed around the resident plant, so that the resident occupied the central 20 × 20-cm plot. The corner plots were planted with *C. bromoides* as a standard check species. The first 10 of the remaining 20 plots were each planted with a ramet of one of the 10 test species, in random sequence. The final 10 plots were occupied by a second ramet of each species, in a different random

sequence. The pattern of planting was the same for all the quadrats corresponding to a given transect line, but differed among lines. The experiment thus involved 30 quadrats holding 600 experimental plants. Planting took place on 5–7 June 1995 and survival was scored on 14 July 1995.

ANALYSIS OF SURVIVAL

At any given site, each species, represented by a single ramet, either died or survived, its score is correspondingly $X_i = 0$ or $X_i = 1$. The general measure of the environment at that site was the total number of survivors $\sum X_i$, from a minimum of 0 to a maximum of 11. The general variance of any two sites with scores $\sum X_{i1}$ and $\sum X_{i2}$ was then estimated as $\frac{1}{2}(\sum X_{i1} - \sum X_{i2})^2$, where X_{ij} is the survival of the i th species at the j th site. However, the composition of these values may differ even if their totals do not; two sites may both have a value of 5, whereas the five species that survived at one site all died at the other. To express this difference in composition, we can decompose the overall environmental variance into two components. For any pair of sites:

$$\frac{1}{2}(\sum X_{i1} - \sum X_{i2})^2 = \sum_i^{\text{species}} \text{Var}(X_i) + N(N-1) \sum_{ij} \text{Cov}(X_{ik}, X_{jk})$$

The first summation on the right-hand side is the mean environmental variance of species, the variance of a given species being $\text{Var}(X_i) = \frac{1}{2}(X_{i1} - X_{i2})^2$. We shall call this quantity the specific variance. The second term is an environmental covariance, the covariance of survival of species between sites. The general variance of survival thus increases as the specific environmental variance and the environmental covariance of survival increase.

Results

ENVIRONMENTAL REPEATABILITY

If individuals of the same genotype tend to resemble one another when growing at the same site, then the score of a clone is a consistent indicator of the variation of environmental conditions from site to site. The clone of *C. bromoides* that was planted into two plots at each site can be used to estimate this environmental repeatability of the 12-month survival of ramets, although the categorical nature of the variable and the availability of only two replicates of a single genotype imply that the estimate will be weak. If there is a consistent tendency for the two replicates at a site to behave in a similar fashion, however, then there will be an excess of sites in which both plants have died or both survived, relative to

Table 1 Repeatability of 1-year survival. Data are number of sites on each transect at which neither (00), one (01) or both (11) of two ramets of clone MSH92-57 of *Carex bromoides* survived. Random location of survivors is tested by chi-square, with significance indicated by * $P < 0.1$, ** $P < 0.01$, *** $P < 0.001$. Final three columns give mean survival, environmental variance σ_E^2 and intraclass correlation t

Transect	00	01	11	χ^2	P	Mean	σ_E^2	t
Lake	7	23	70	5.7	*	0.815	0.0367	0.24
Gorge	54	34	12	3.3	*	0.290	0.0371	0.18
Cliff	45	26	28	20.8	***	0.414	0.1131	0.46
Overall	106	83	110	59.3	***	0.507	0.11175	0.45

the expected frequency of such sites, given that survival or death occur at random. Chi-square analysis showed that this occurred on all three transects and was highly significant when data from all three transects were pooled (Table 1). A single-classification analysis of variance yields estimates of the among-site or environmental variance σ_E^2 and the within-site or error variance σ_e^2 . A quantitative measure of correlation can then be obtained as the intraclass correlation coefficient $\sigma_E^2/(\sigma_E^2 + \sigma_e^2)$. It was moderately large (0.46) on the Lake transect, smaller (0.24, 0.18) on the other two, and again moderately large (0.45) in the pooled data.

The overall survival of the set of 11 species can be used to predict the diversity of the resident assemblage in two ways. First, diversity might vary with scale: there should be more species where there are more individuals. Sites with high ramet survival should have many resident individuals and therefore many resident species. Secondly, diversity might vary with structure: combinations of sites with greater environmental variance of survival may support more resident species. We can also distinguish between general and specific effects. Both scale and structure may refer to the general (overall) survival of the set of 11 experimental species, or to the specific survival of each of these species.

GENERAL ENVIRONMENTAL QUALITY

Overall mean survival

The number of surviving individuals of each species on each transect is given in Table 2. Overall annual survival was $1166/3300 = 0.353$. This may be compared with the density of natural populations. In any given area, the number of resident plants n_p will be the product of the annual number of incomers n_i and their annual survival rate u , summed over years:

$$n_p = n_i \sum_{x=1}^{\infty} u^x = n_i u / (1 - u)$$

This number will vary with scale, but there will be some characteristic dispersal scale at which a single incomer appears every year, to yield a mean density

of $u/(1 - u)$, equal to 0.546 for our experimental data. (The incomer is in this case a ramet that has not only reached a site but has succeeded in establishing itself there.) The census of the native *Carex* flora yielded a total of 5460 records (of adult plants identified to species and of unidentified juveniles) from 3364 plots. Although each record represented the presence or absence of a species in the plot rather than the number of individuals, because vegetative growth made it impracticable to recognize or count individuals where stems were close together, there was usually only a single individual per plot. The mean density of records at this scale was thus $5460/12000 = 0.455$. This was quite close to the expected value, suggesting that, by chance, our sampling unit of 2×2 m corresponded rather closely to the characteristic dispersal scale of *Carex* ramets. If dispersal were random, one would expect a fraction

Table 2 Survival of transplanted ramets on the transect lines

Species	Lake	Gorge	Cliff	Total
app	83	12	39	134
arc	16	9	0	25
bro	95	38	30	163
com	74	6	8	88
dew	62	6	11	79
gra	87	14	10	111
luc	48	14	21	83
ped	77	32	56	165
pen	78	1	28	107
ros	62	8	30	100
spr	66	38	7	111
Total	748	178	240	1166

The species used are as follows: app, *Carex appalachica* J.M. Webber & P. Ball; arc, *Carex arctata* W. Boott; bro, *Carex bromoides* Willd.; com, *Carex communis* Bailey; dew, *Carex deweyana* Schwein.; gra, *Carex gracillima* Schwein.; luc, *Carex lucorum* Willd.; ped, *Carex pedunculata* Willd.; pen, *Carex pensylvanica* Lam.; ros, *Carex rosea* Schk.; spr, *Carex spengelii* Dewey.

Carex lucorum and *Carex pensylvanica* are often difficult to distinguish at this locality, but we chose clones for which species assignment was unequivocal.

$1 - e^{-0.455} = 0.366$ of the plots to be occupied by at least one *Carex* species. The actual value of $3364/12000 = 0.280$ was rather lower, indicating that *Carex* tends to be rather strongly aggregated.

Abundance and diversity

Survival varied among species and among transects (Table 2). Variance among species is relevant to the problem of abundance: to what extent can the abundance of species in the resident assemblage be predicted from their performance on the transects? Variance among transects, or among sites within transects, is relevant to the problem of diversity: to what extent can the diversity of the resident assemblage be predicted from environmental quality or environmental heterogeneity as measured by the transect material?

Species diversity among the transects

The extended quantitative survey of *Carex* assemblages on 24 1-km lines yielded a total of 4758 identifiable adult individuals belonging to 27 species, with an average of 12.08 species per line. A similar survey was carried out along the transects. This yielded 380 identifiable individuals belonging to 20 species, including nine of the set of 11 species used to estimate environmental variance. The relationship between the number of species S and the number of individuals s among the survey lines was found to be: $\log S = 0.201 \log s + 0.636$. The predicted number of species in a sample of 380 individuals is thus 14.3. The observed excess was largely attributable to the Lake transect, which had many more species than predicted (17 vs. 12).

Species diversity and environmental quality

All pair-wise comparisons among the transect lines showed significant differences in total survival at $P < 0.01$. Survival was much greater on the Lake transect ($u = 0.680$) than on either of the other two, the Cliff transect ($u = 0.218$) having a somewhat greater value than the Gorge transect ($u = 0.162$). Variation in observed species diversity, relative to that expected from the number of individuals scored, was therefore related to variation in environmental quality among transects.

Overall survival also varied from site to site within each transect (Fig. 2). The correlation between the number of experimental plants surviving at a site and the number of individuals or species of resident plants found at that site was positive and significant (or very close to significance, at $P = 0.05$) on all three transects (Fig. 3). This demonstrated some degree of correspondence between plant response and the native assemblage at a scale of

10 m. The correlations were uniformly weak, however, with shallow slopes and positive intercepts.

General environmental structure

The spatial structure of the environment is expressed by the way in which the overall environmental variance increases with distance. We regressed log variance, V , on log distance, D , for equal log distance intervals for all possible pair-wise combinations of sites to estimate the slope of the power law, $V = aD^z$ (Bell *et al.* 1993). The null hypothesis of no systematic tendency for variance to increase with distance was constructed by re-allocating the 100 values of overall survival to sites at random, then regressing log variance on log distance; repeating this simulation 100 times gave a slope and standard deviation expressing the structure of a random environment. In all cases, this procedure yielded a mean value of slope close to zero, as expected. The slope of the data was positive and significant ($P < 0.01$) on all three transects, showing them to be structured on scales between 10 m and 1000 m (Fig. 4). However, the slope was much greater on the Cliff ($z = +0.156$) and Lake ($z = +0.128$) transects than on the Gorge transect ($z = +0.065$). At a scale of 10 m, the Lake and Gorge transects had about equal variance, and both were more variable than the Cliff transect. Because variance increased sharply with distance on the Cliff and Lake transects, but not on the Gorge, the Lake transect was more variable above 100–200 m than either the Cliff or the Gorge transects, which were similar at this scale. Another way of expressing this is to say that the Lake and Cliff transects were relatively coarse-grained, the Lake being the more heterogeneous at all scales, whereas the Gorge transect was a more fine-grained environment.

Physical factors

The heterogeneity and structure of the three transects with respect to canopy cover, ground cover and soil pH are summarized in Table 3. The ranking of the transects varied according to the factor considered. The Lake was the most variable for soil pH, the Cliff for ground cover, and the Gorge for canopy cover. The regressions for ground cover and soil pH were steeper on the Cliff transect than on the other two, but for canopy cover the regression was steepest on the Gorge transect.

Species diversity and environmental structure within the transects

The response of species diversity to environmental structure hinges on the behaviour of the specific covariance. Laboratory studies of microbes have shown

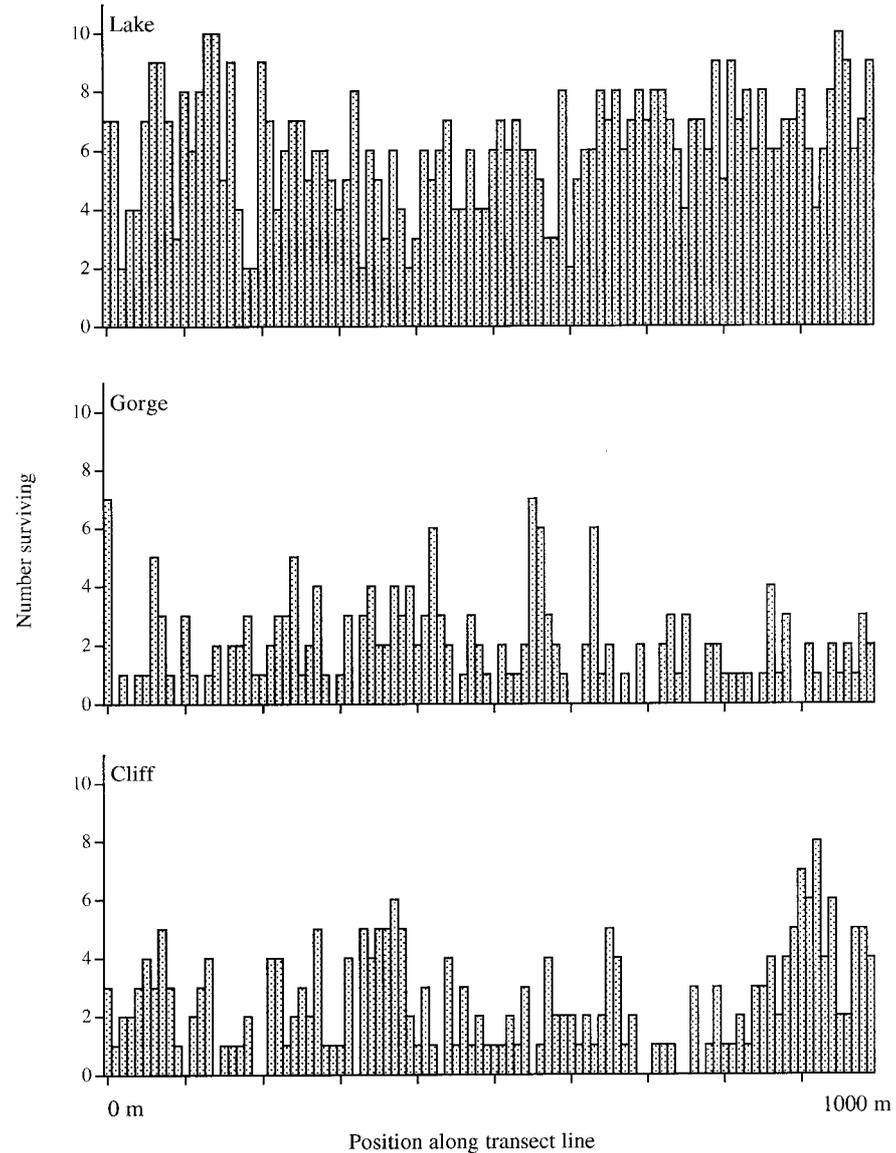


Fig. 2 Plant survival along the transect lines. The columns show the number of plants surviving from the standard set of 11 test species at 10-m intervals along each line.

Table 3 Structure of the physical environment along the transects. The coefficients refer to the regression of log-variance on log-distance

		Transect		
		Lake	Gorge	Cliff
Ground cover	Regression b	+0.138	+0.171	+0.279
	Correlation r	+0.66	+0.70	+0.83
Canopy cover	Regression b	+0.075	+0.257	+0.160
	Correlation r	+0.41	+0.78	+0.61
Soil pH	Regression b	+0.092	+0.028	+0.237
	Correlation r	+0.39	+0.15	+0.69

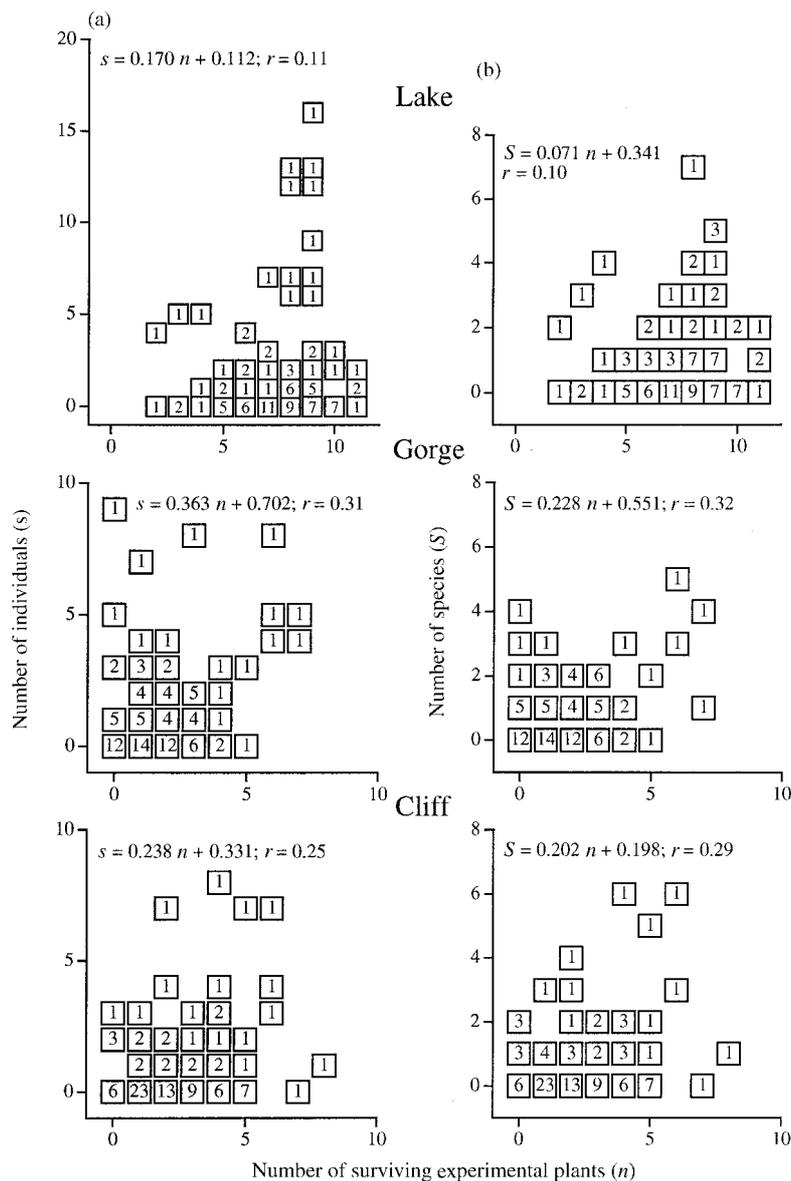


Fig. 3 Abundance and diversity of the local *Carex* community in relation to the survival of ramets. (a) Abundance. Number of resident individuals s as a function of number of ramets surviving in 10-m segments of transect lines. (b) Diversity. Number of species S as a function of number of ramets surviving in 10-m segments of transect lines.

that the specific, or genetic, correlation of performance falls as the general environmental variance increases (Bell 1992), i.e. the ranking of species in the two environments becomes more similar as mean performance in the two environments becomes more similar. This generalization was tested for the *Carex* system by dividing each transect into 50-m sections, within each of which total survival might take any value between 0 and 55. The general environmental variance increased with distance (Fig. 5a, and above), whereas the specific correlation fell with distance (Fig. 5b). This was because the specific correlation of survival fell as general environmental variance increased (Figs 5c,d), extending the laboratory result to a completely different field situation.

This will be translated into an effect on species diversity through selection, because the composition of the assemblage at any given site will depend to some extent on the relative fitness of species at that site. The specific correlation of occurrence will then fall as environmental variance increases, causing an increase in species diversity. To evaluate the effect of environmental heterogeneity on species diversity, we calculated the mean species diversity for each pairwise combination of sites within a given distance category. This quantity was then regressed on the environmental variance previously calculated for the same distance category. This provided an estimate of the relationship between species diversity and environmental heterogeneity independent of the

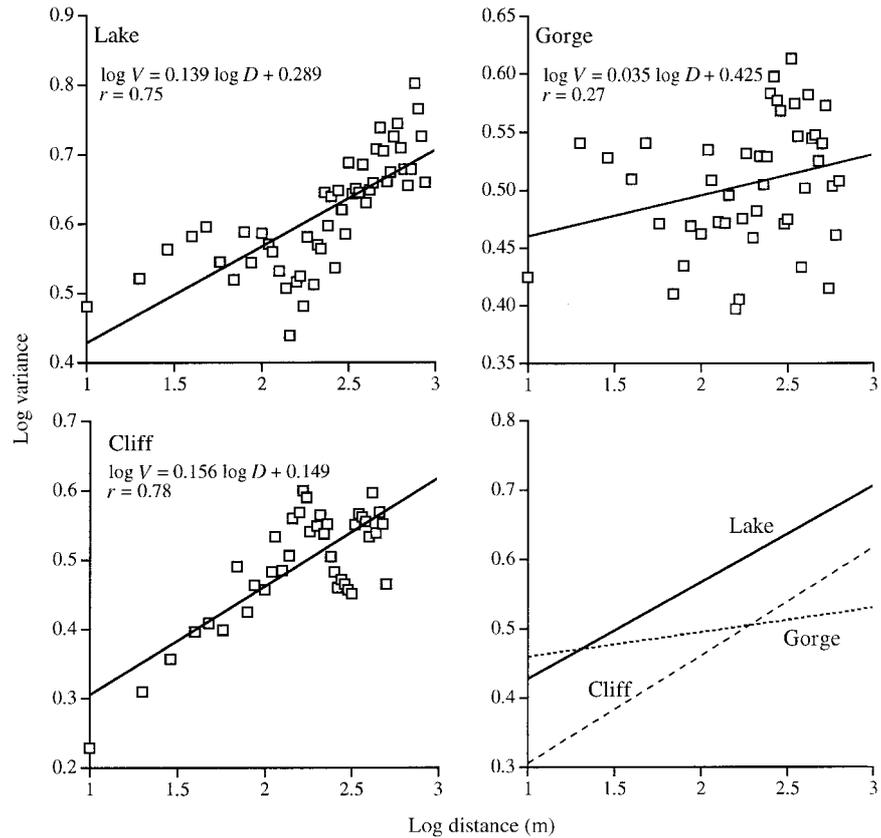


Fig. 4 The general spatial structure of the transect lines. Data are log-general variance of 1-year survival for all pair-wise combinations of sites at equal log-distance classes. The fourth graph is a composite showing the regressions for all three transect lines.

mean value of the environment, as the mean value at sites will not vary systematically with their separation. The results are shown in Fig. 6. The regression on general variance was positive in all three transects, with an average slope of about +0.1.

SPECIFIC ENVIRONMENTAL QUALITY

Variance among species

Overall survival varied among species from a minimum of 0.083 for *C. communis* to a maximum of 0.543 for *C. bromoides*. The species-specific survival rates measured on the transects can be compared with the species abundances estimated in the census (Fig. 7). There was no tendency for species that survived better on the transect lines to be more abundant in the assemblage. Indeed, any tendency among the standard set of 11 species was slightly negative ($r = -0.35$): *C. communis* was a very abundant species in the forest, whereas *C. bromoides* was rare.

Specific environmental quality

If the particular characteristics of a site favour some species over others, then the species should tend to

occur at those sites where they survive as implanted ramets. The relationship between species distribution and species performance on the transect lines is shown in Table 4. Entries along the leading diagonal represent cases in which a species occurred naturally at a site where the implanted ramet of that species survived; these cases totalled 43. The expected number of cases is readily obtained from the product of row and column frequencies; these totalled 44.3. There was therefore no evidence that species tend to occur predominantly at the sites to which they are best adapted, at the scale of 10 m.

The results of the targeted implant experiment are given in Table 5. Overall survival after 12 months was $277/600 = 0.462$, substantially and significantly greater than that of ramets planted into random sites along the transect lines ($\chi^2 = 30.8$, d.f. = 1, $P < 0.001$). This presumably means that sites already occupied by *Carex* tend to be more suitable than random sites for the growth of *Carex*. There was no sign of a specific effect, however. The experiment can be interpreted like the transect results: implants are expected to survive better in 'home' sites, so entries along the leading diagonal should exceed the number expected by chance. In this case,

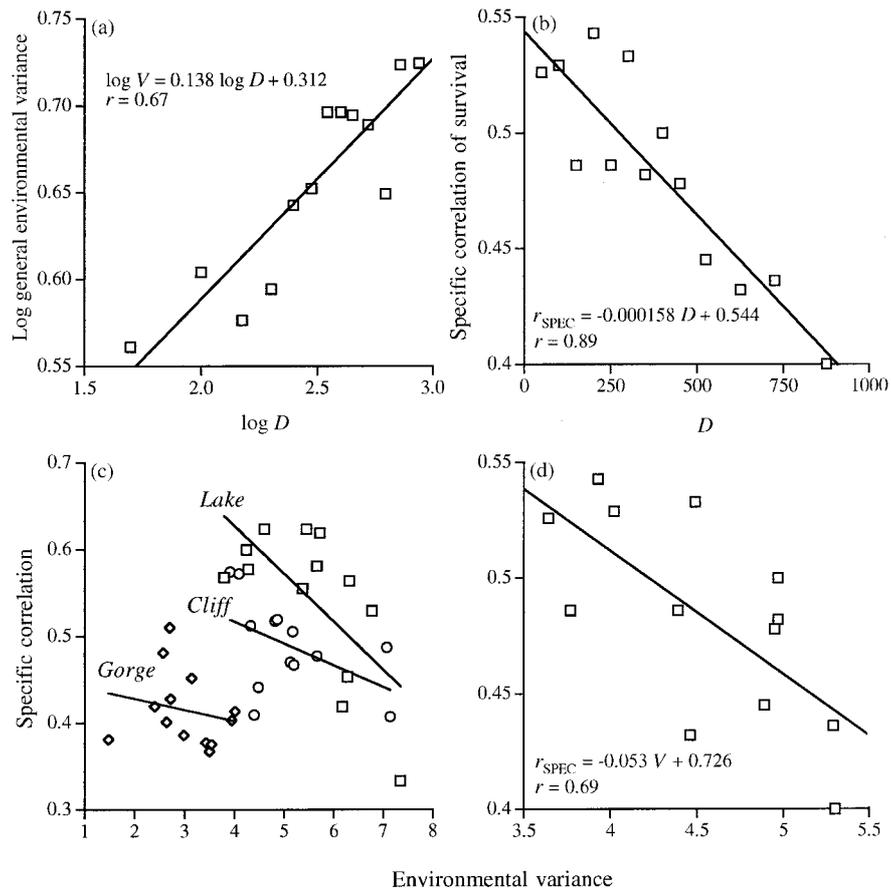


Fig. 5 The decline of the specific correlation of performance with increasing general environmental variance. The analyses refer to 50-m segments of the transects. Plotted points are means over all three transects, except in (c). (a) The general environmental variance of two sites increased with their distance (m) apart (cf. Fig. 4). (b) The specific correlation of two sites decreased with their distance (m) apart. (c) The specific correlation fell as environmental variance increased on all three transects. (d) The overall regression of mean values fell as environmental variance increased.

these entries totalled 28, against an expected value of 27.1. The mean survival on home sites, $28/60 = 0.467$, was in fact as close as possible to the overall mean survival, $277/600 = 0.462$. Thus, this experiment failed to demonstrate that species are best adapted to the sites at which they occur, at the scale of 1 m.

Specific environmental structure and species diversity

The specific variance (mean environmental variance of species) also increased with distance on the Lake and Cliff transects, suggesting that these environments may be structured in different ways for different species (Fig. 8). Although the fit of the data to

Table 4 Relationship between the survival of experimental ramets of a species and its occurrence in the local community. A unit entry in the table signifies that a given species occurred naturally at a 10-m site where the test ramet of that species survived. The data are pooled over all three transects

Resident species	Experimental species surviving at site							Total
	arc	com	dew	gra	ped	pen	ros	
arc	0	4	5	6	13	6	5	39
com	0	12	14	19	21	15	14	95
dew	0	2	3	2	6	1	2	16
gra	0	0	1	1	1	1	1	5
ped	1	11	12	19	26	12	13	94
pen	0	0	1	1	5	0	2	9
ros	3	2	3	1	5	2	1	17
Total	4	31	39	49	77	37	38	275

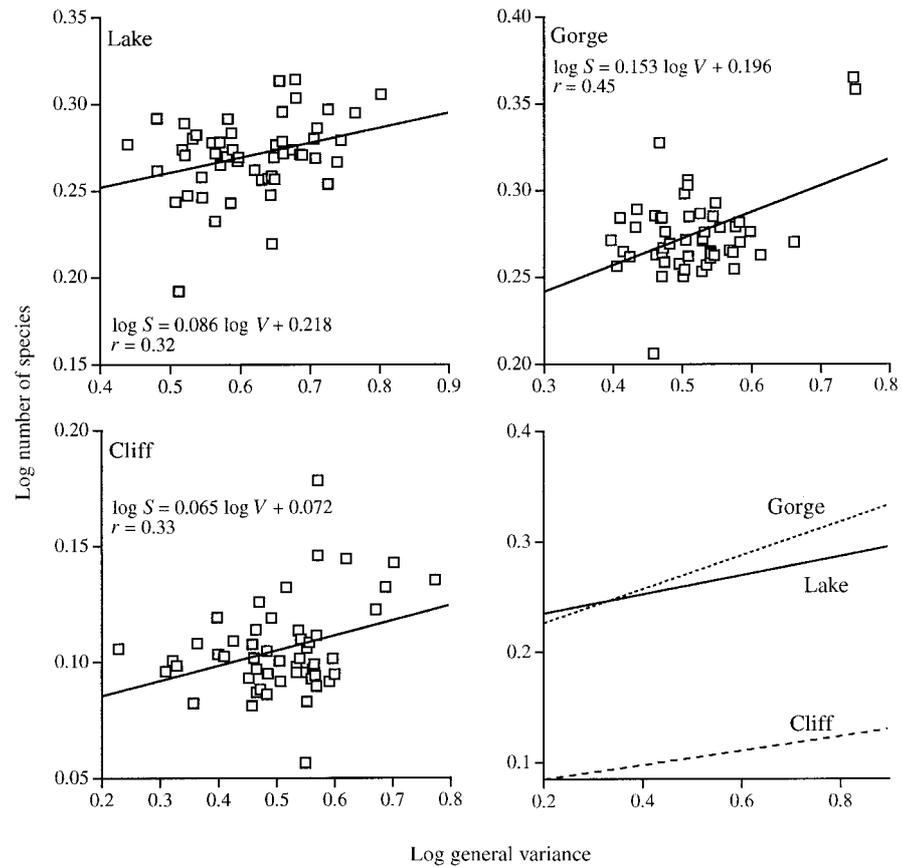


Fig. 6 The relationship between species diversity and environmental heterogeneity. The analysis refers to the general variance and the combined diversity of pairs of 10-m sites.

the regressions was about as good for the specific variance as for the general variance, the slopes were substantially lower for the specific variance: +0.036 as opposed to +0.139 for the Lake transect, and

+0.061 as opposed to +0.142 for the Cliff transect. On the Gorge transect, there was no discernible tendency for the specific variance to increase with distance. The regression of species diversity on specific

Table 5 Results of targeted implant experiment. Entries in the table are the number of ramets of a given species (row) surviving when implanted close to a resident plant of the same or different species (column)

Incomer	Resident										Total
	arc	bac	dew	gra	lax	luc	ped	pen	pla	spr	
arc	3	4	1	3	5	2	3	4	3	6	34
bac	4	3	2	4	3	2	4	6	2	4	34
dew	1	2	2	1	0	0	2	4	2	2	16
gra	4	3	5	4	5	3	4	6	3	5	42
lax	4	3	4	1	3	1	2	6	5	2	31
luc	2	2	2	3	4	0	2	6	1	3	25
ped	5	2	4	4	4	1	2	6	5	0	33
pen	2	1	1	1	3	0	2	6	3	2	21
pla	3	2	1	2	3	1	1	5	3	2	23
spr	2	0	2	1	2	1	1	4	3	2	18
Total	30	22	24	24	32	11	23	53	30	28	277

The three species not appearing in Table 2 are: bac, *Carex backii* F. Boott; lax, *Carex laxiflora* Lam.; pla, *Carex plantaginea* Lam.

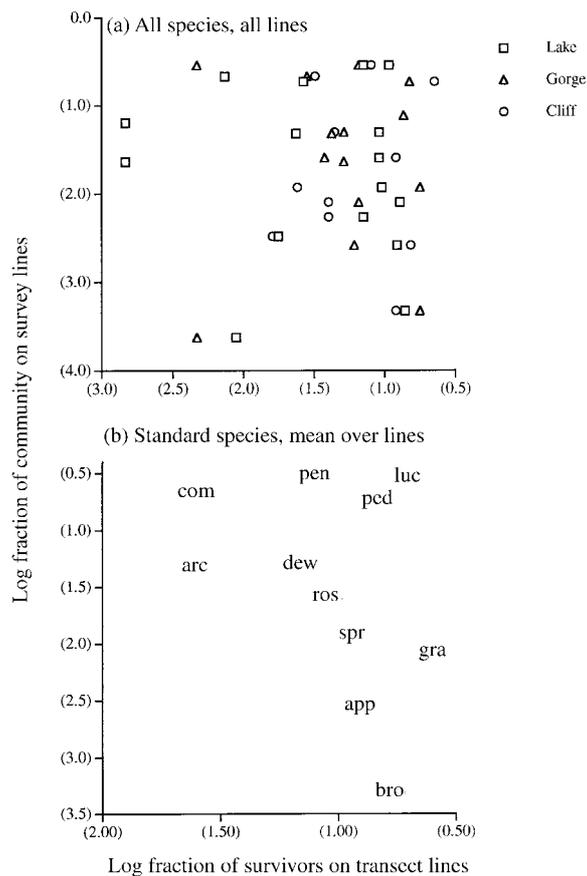


Fig. 7 The relationship between survival of the experimental plants and community composition. The *x*-axis is the number of transplanted ramets of a given species surviving on a line as a fraction of the total number of ramets surviving on that line. A total of 4100 ramets was scored. The *y*-axis is the number of plants of a given species found on the 24 survey lines as a fraction of the total number of plants found on the survey lines. For the 15 species set out on the transect lines, a total of 4233 plants was found on the survey lines. (a) Each point is the value for a given species on a given line: squares, Lake transect; triangles, Gorge transect; circles, Cliff transect. (b) Unweighted mean over the three transect lines for the standard set of 11 species.

variance was strongly positive on the Cliff transect (+0.27), weakly positive on the Lake transect (+0.086) but negative on the Gorge transect.

Stability analysis

The results so far have shown that diversity increases with general environmental quality and with variance in general environmental quality. However, whereas diversity did seem to increase with specific environmental variance on two of the transects, there was no discernible tendency for the distribution of species to be correlated with their performance at a particular site. This suggests that species may be responding in different ways to general environmental quality, rather than being closely adapted to different particular attributes of microhabitats. The stability analysis developed by agronomists (reviewed by Lin *et al.* 1986) can be used to describe the response of species to general environ-

mental variance. The mean value of a site is equated with the mean response of plants at that site, in this case their mean survival. The regression of species-specific survival on mean survival over sites is then a measure of stability: a shallow regression indicates a lack of response to increasing environmental quality and thus a stable species, whereas a steep regression is characteristic of a species with greater sensitivity or responsiveness to variation in environmental quality. The average regression is necessarily unity. The variation of regression slopes among species is one component of the species-sites interaction variance, the other being the deviation from linearity, which may represent non-linearity or (more probably) idiosyncratic responses to particular attributes of sites.

This procedure is exemplified in Fig. 9 by data from *C. pedunculata* and *C. gracillima*. Mean survival over all 11 experimental species was relatively low on the Gorge and Cliff transects, where *C. ped-*

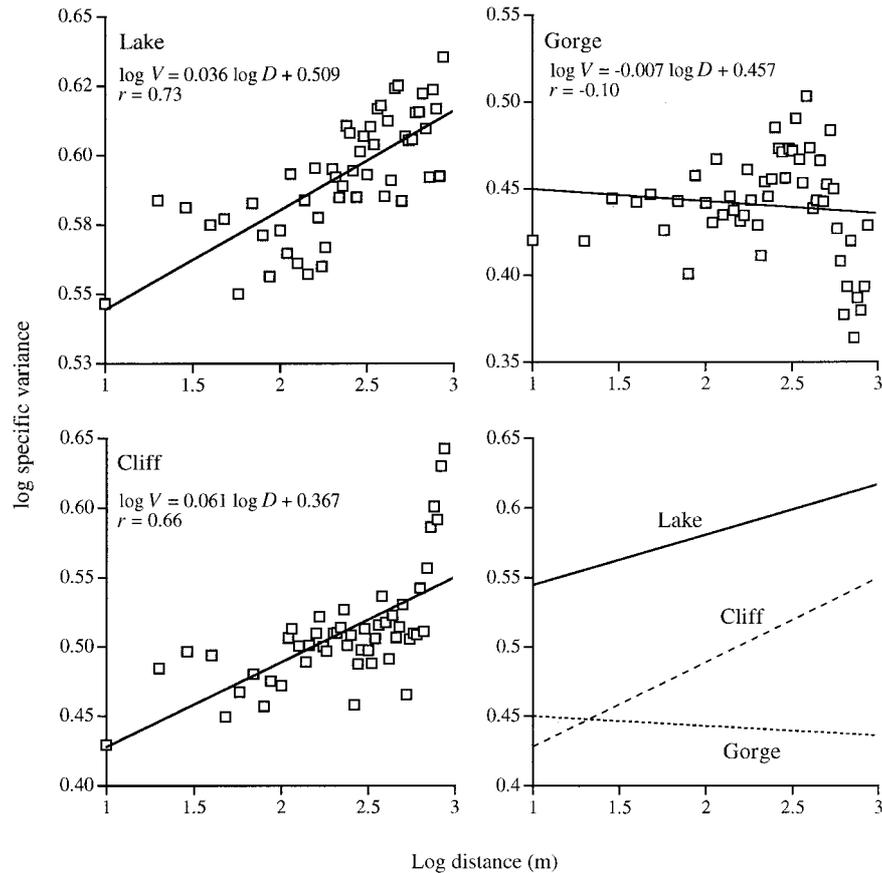


Fig. 8 The specific spatial structure of the transect lines. Data are log-specific variance of 1-year survival for all pair-wise combinations of sites at equal log-distance classes. The fourth graph is a composite showing the regressions for all three transect lines.

unculata had the higher rate of survival. Mean survival was greater on the Lake transect, where *C. gra-*

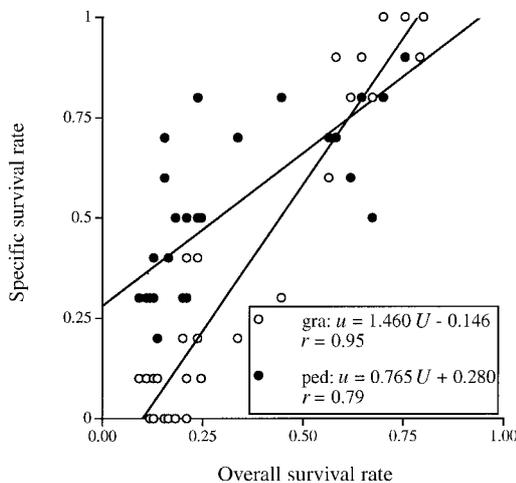


Fig. 9 Stability analysis for two species of *Carex*.

cillima survived better. Putting these two together shows how *C. pedunculata* was the more stable species, with a relatively shallow regression ($b = 0.75$), whereas *C. gracillima* was the more responsive species, with a steeper regression ($b = 1.46$). The two regressions crossed at a mean survival of 0.605, *C. pedunculata* having the greater survival in poorer sites and *C. gracillima* the greater survival in better sites. Note that the correlation of survival between these two species will be positive over a narrow range of sites falling either to one side or the other of the intersection at 0.605, but negative over a broader range of sites spanning the point of intersection, i.e. the species correlation will tend to fall as general environmental variance increases. The greater responsiveness of *C. gracillima* implies that it should vary more widely in abundance in natural assemblages. This was the case: when abundance on a survey line was expressed as a fraction of the total abundance of the species over all lines, the variance of abundance was $p \sim = 0.00908$ for *C. gracillima*, compared with $p \sim = 0.00114$ for *C. pedunculata*. The response of the experimental plants to mean

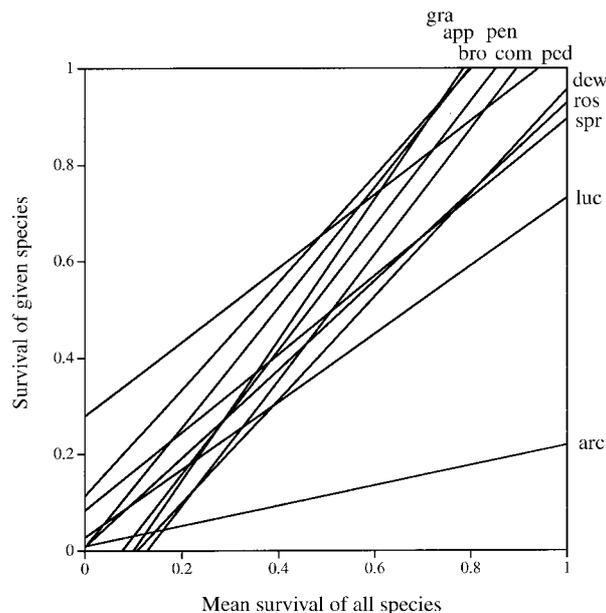


Fig. 10 The general stability analysis. The basis of the analysis is ramet survival on 50-m segments of the transect lines.

environmental quality thus predicts the dispersion of species in natural assemblages.

The stability regressions for all 11 species are shown in Fig. 10. They intersected extensively, showing that the ranking of species changes with variation in general environmental quality. These

regressions can be used to calculate the expected value of survival for a given species at any level of mean survival. This value reflects the linear response of the species to mean environmental quality, neglecting any non-linear response and any specific response to other environmental factors at a given site. For any pair of levels, we can calculate the general environmental variance and the specific correlation. The relationship between the specific correlation and general environmental variance can then be evaluated over all pair-wise combinations of levels (Fig. 11). The specific correlation falls steadily from +1 as the difference in mean environmental quality increases, approaching zero when very poor and very good sites are compared.

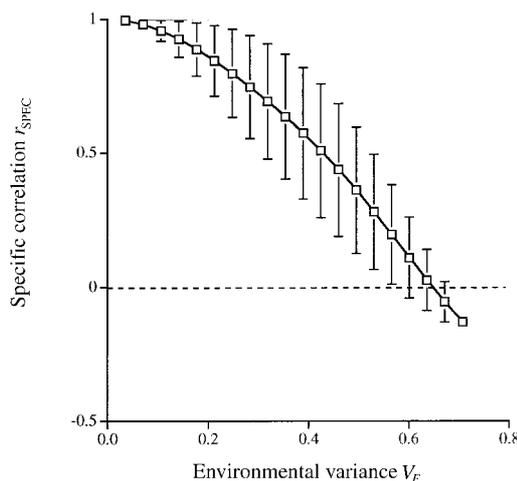


Fig. 11 The stability structure of the transects. The linear estimate of ramet survival for each species from the stability regressions is used in place of the observed value. These estimates were obtained for values of mean survival at intervals of 0.05. The specific correlation is calculated on these values for each pair-wise combination of values. The combination of values itself defines an environmental variance. The bars are ± 1 SD of the estimates for each pair of values.

Discussion

ENVIRONMENTAL HETEROGENEITY

In the past, geostatistical techniques have usually been applied to measurements of physical factors, which provide a simple and precise description of environmental structure that is relatively easy to obtain. However, different factors may yield different descriptions, and it is difficult to know in advance which is the most appropriate to relate to biological diversity. We have attempted to avoid these difficulties by using the response of native plants as the measure of the environment. Our experimental transects represent, in effect, huge multi-channel instruments laid over the surface of the landscape to give a true description of how the forest floor varies from site to site from the point of

view of a particular group of native organisms. They have shown that the environment is indeed structured, on scales relevant to the growth and dispersal of forest plants. The small-scale heterogeneity of the environment shown by measurements of physical factors and explant trials is thereby confirmed, and extended to larger scales. Such experiments enable us to compare the heterogeneity and structure of areas in a biologically meaningful way; thus, from the point of view of the sedge assemblage, the Lake transect is more heterogeneous at all scales than the Cliff transect, and the Lake and Cliff transects are more coarse-grained than the Gorge transect.

We suggest that this approach can be used to provide species-based definitions of habitats and the assemblages that inhabit them.

1 Two sites represent different habitats with respect to a defined set of organisms if the specific correlation of performance among the members of this set is negative. From our experimental data, the specific correlation of performance is known to fall with distance. The distance at which the regression of correlation on distance reaches zero, i.e. the correlation changes from positive to negative, is the spatial scale of a habitat. Within a habitat, selection will be directional and will thus tend to create uniformity; among habitats, selection will be to some extent disruptive, and may sustain diversity.

2 The organisms present at two sites represent different assemblages if the specific correlation of occurrence is negative. From our observational data, the specific correlation of occurrence also falls with distance, and the point at which it reaches zero is the spatial scale of an assemblage.

To the extent that different assemblages occupy different habitats, we expect the spatial scales of habitats and assemblages to be related. In our data, the specific correlations of both performance and occurrence approached zero only at distances approaching 1 km, the limit of our samples. This suggests that, from the point of view of *Carex*, the forest at Mont St Hilaire is a single habitat supporting a single assemblage, despite the quantitative variation among sites within the forest that we have documented.

DIVERSITY AND GENERAL ENVIRONMENTAL VARIANCE

To the extent that species tend to be well-adapted to the particular sites where they occur, the specific covariance of occurrence among sites will be created, through selection, by the specific covariance of performance among sites. Diversity will therefore increase with environmental heterogeneity only if the specific covariance of performance decreases as environmental variance increases, and only if this

effect is translated into a reduction of the specific covariance of occurrence.

Our experiments have demonstrated for the first time a correlation between species diversity and a species-defined measure of environmental heterogeneity. There is a suggestion that this is apparent when the three transects are compared: the Lake transect is the most heterogeneous at all scales, and the resident assemblage comprises more species, relative to the number expected from the number of individuals sampled, than that of the other two transects. The evidence for a relationship between species diversity and environmental heterogeneity within each transect is more convincing, however, especially for the general variance.

Our results, combined with previous work, lead us to suggest a general interpretation of species diversity in our forest *Carex* system as a series of linked propositions, which are set out in Fig. 12.

(a) The variance of physical and chemical characteristics of the environment increases with distance, creating environmental heterogeneity at scales relevant to the growth and dispersal of forest plants (Lechowicz & Bell 1991).

(b) Plant growth responds to this heterogeneity in both glasshouse (Lechowicz & Bell 1991) and field (Schoen, Bell & Lechowicz 1994) trials.

(c) From (a) and (b) it is expected that the variance of biologically important characteristics of the environment should increase with distance, as has been shown by the survival response of *Carex* implants (this paper), yielding a species-defined measure of environmental heterogeneity.

(d) The covariance of fitness measures among species decreases as the general environmental variance increases, as observed in laboratory trials with micro-organisms (Bell 1992) and in field trials with *Carex* (this paper).

(e) Combining (c) and (d), the specific covariance of performance in any pair of sites decreases with their distance apart (this paper).

(f) Through selection, (d) will cause the specific covariance of occurrence to fall as environmental variance increases.

(g) The consequence of (f) is that species diversity will increase as the environmental variance of sites or combinations of sites of fixed area increases (this paper).

(h) Through selection, (e) will cause the specific covariance of occurrence to decrease as the distance between sites increases.

(i) From (h), the combined diversity of any pair of sites will tend to increase with their distance apart. Propositions (g) and (i) are closely related, because (c), environmental variance, increases with distance.

Furthermore, it follows from (i) that the diversity of a site will increase with its area, the well-known species-area rule (j). This is not only a function of

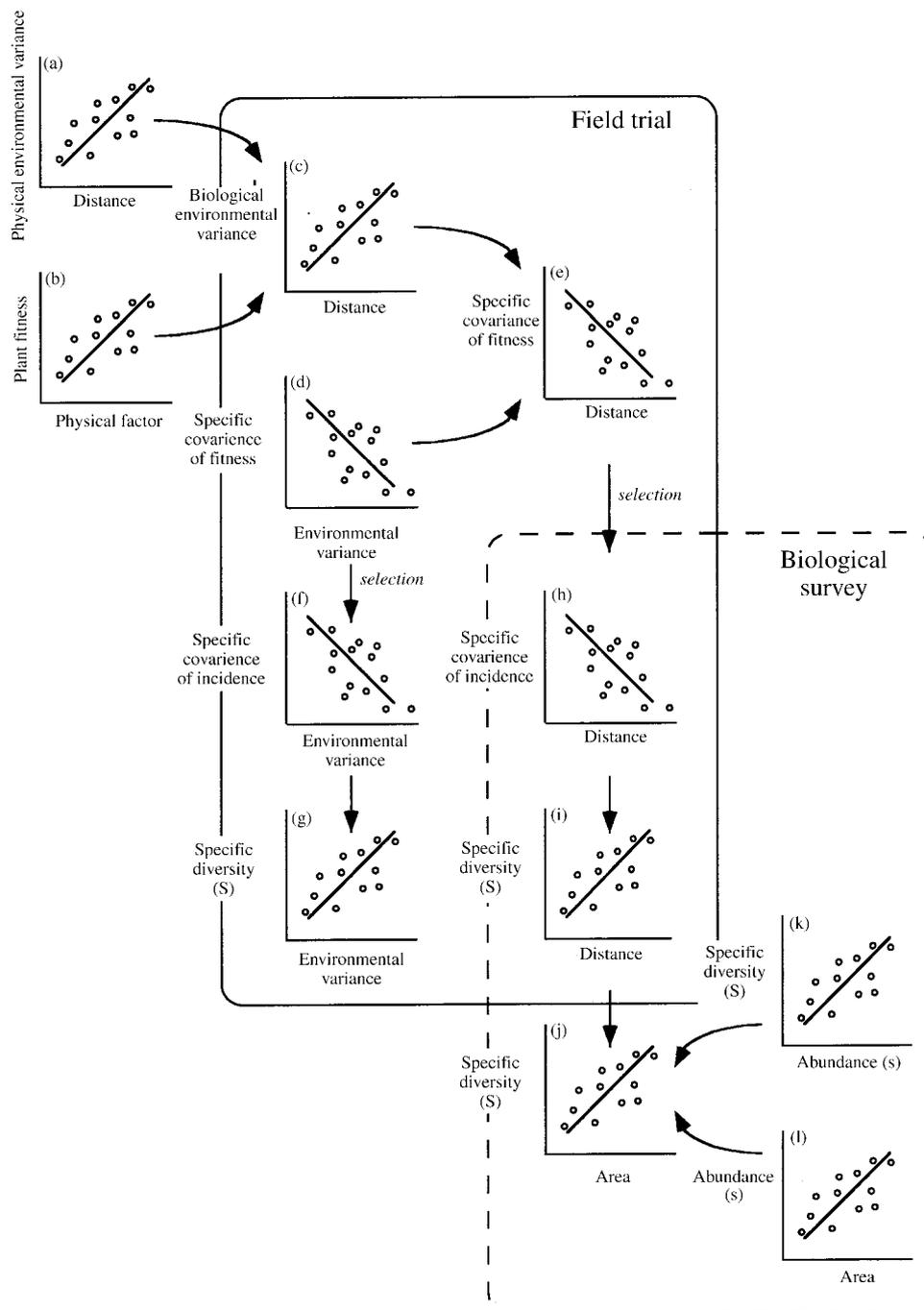


Fig. 12 The system of hypotheses connecting species diversity to environmental heterogeneity.

structure, however, but is also an effect of scale. The number of species found will increase with the number of individuals sampled (*k*), which will in turn increase with the area searched (*l*). Species diversity will therefore increase with area even in random samples from unstructured environments. Our results demonstrate that both scale and structure contribute to the species–area relationship (compare with Palmer & White 1994).

Some of the propositions in Fig. 12 can be established only by experimental investigations in the

kind of field trial described in this paper. The remaining part can be established through a biological survey.

THE MARGINAL-SPECIALIST MODEL

The niche-separation model predicts that global abundance (abundance in the forest as a whole) should depend on the frequency of sites to which a species is well adapted. If the three transect lines are a fair sample of forest sites, therefore global abun-

dance should be predicted by the overall survival of ramets. This was not the case. Moreover, the theory also requires the existence of two or more distinct habitats, and therefore predicts that the specific correlation should become negative at intermediate spatial scales. This was not observed. The niche-separation model therefore does not provide a satisfactory interpretation of our results.

The productivity of random sites is relatively low, as shown by the higher survival of the targeted implants. The other theory outlined in Fig. 1 (the rare-generalist model) then predicts the lack of correlation between global abundance and the performance of random implants. It is also consistent with the behaviour of the specific correlation, which falls with distance but remains positive, except, perhaps, near the limit of our experimental design at distances approaching 1 km. A further prediction made by this theory, however, is that the species with the greatest local abundance have the smallest range, whereas species with broad ranges are everywhere sparse. There should therefore be a negative correlation between mean local abundance (at those sites where a given species occurs) and range (the number of sites occupied). The reverse holds in most cases (see Gaston 1996; but Thompson *et al.* 1998 found no correlation in the British flora), and in our *Carex* system in particular range and abundance were positively correlated. The rare-generalist model must therefore be rejected.

To explain our results, we have devised a further model, shown in the lowest panel of Fig. 1. The species that dominate the most productive sites also have the broadest ranges: other species have a superior performance only in a narrow range of unproductive sites. We call this the marginal-specialist model. It incorporates a positive correlation between local abundance and range, as the data require. Like the rare-generalist model, it predicts the lack of relationship between global abundance and survival in random sites, and the tendency for the specific covariance to remain positive at intermediate spatial scales. It seems to be consistent, therefore, with patterns that are associated with the general environmental variance. It also resembles the rare-generalist model in predicting the existence of nested subsets of species (Wright & Reeves 1992; Cook 1995).

DIVERSITY AND SPECIFIC ENVIRONMENTAL VARIANCE

The specific variance was also structured, but increased with distance much less rapidly than the general environmental variance. In other words, the forest landscape was relatively coarse-grained with respect to general conditions of growth, and more fine-grained with respect to environmental factors that affect species differentially. Thus, much of the

environmental heterogeneity to which sedges respond differentially may occur at scales below our 10-m sampling scale. We have no evidence that this is the case, however. On the contrary, there was no correspondence between occurrence and performance either on the transects, at scales of up to 5 m, or at the targeted implant sites, at scales of 1 m or less. There appears to be no precise local adaptation: the assemblage was not at equilibrium with the landscape at the taxonomic and geographical scales that this study encompassed. The failure of these experiments seems puzzling, in the light of the relationship between diversity and environmental structure. It may be attributable simply to their low power. Given the sample sizes involved and the rate of survival at non-home sites in the targeted implant experiment, we can calculate the least value of survival at home sites that would be detected in 90% of cases at $P = 0.05$ (equations 23.76–23.78 in Zar 1996). The result is a value of 0.70, far in excess of the value of 0.46 found in non-home sites. The experiment was therefore capable of detecting only very pronounced local adaptation. Another way of expressing this is to ask how large the experiment would have to be in order to detect a 10% increase in survival at home sites, from 0.46 to 0.506, at $P = 0.05$ in 90% of cases. The answer is that it would be necessary to use 87 replicates of each species (rather than three), implanting a total of over 17 000 ramets (rather than 600). Clearly, no practicable experiment of this kind can either detect reliably or reject convincingly a modest degree of local adaptation.

There is better evidence that the species respond differently to general environmental variance, with some being more stable and others more responsive. The relative survival rates of the species thus change as one moves from poor sites with low overall survival to good sites with high overall survival, so that species composition responds to coarse-grained general environmental structure rather than to fine-grained specific structure. The consequence of this component of the species–sites interaction is that the specific correlation of performance falls as the general environmental variance increases (Figs 5 and 12). This supplies the mechanism for the observed increase in species diversity with distance between sites, and suggests that in this case the marginal-specialist model might provide a reasonable explanation for the maintenance of diversity.

In conclusion, we have shown that the forest environment is structured, that the specific correlation of performance falls as general environmental variance increases, and that species diversity increases with environmental heterogeneity. At the same time, we have also shown that the forest floor is not a simple mosaic of discrete habitats to which species become differently adapted. Instead, species

responded differently to continuous variation in environmental quality. There were cases where this differentiation was relatively strong, and disruptive selection may maintain some level of diversity (for example Fig. 9). Nevertheless, we have not been able to establish convincingly that selection in a heterogeneous environment alone provides an adequate mechanism for the maintenance of observed levels of diversity. A large part of this diversity seems to consist of species that are only slightly differentiated and that are not restricted to distinctive kinds of site. It is presumably maintained by recurrent migration that is not effectively opposed by selection which is either perennially weak or fluctuates in time. We emphasize that a different result might be obtained at different scales of investigation. If we had studied a greater variety of sites, including wetland and ruderal sites, or included a greater variety of taxa, outside the single genus *Carex*, we might have observed patterns of assemblage composition related to differential survival. It may be generally true that related species growing under similar conditions respond primarily to quantitative variation in the environment in a way best described by the marginal-specialist model, whereas at larger genetic and ecological scales qualitative variation in the environment giving rise to negative specific correlations creates stronger and more specific selection that is best described by the niche-separation model.

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