

## Chapter 6

# The scale of local adaptation in forest plants

G. Bell,\*† M. J. Lechowicz\* and M. J. Waterway‡

### Introduction: theories of distribution and abundance

Distribution and abundance are the central themes of community ecology. They emerge from biological surveys in which the organisms collected or recorded from a number of sites are assigned to taxa, typically species. The output of a biological survey is thus a species  $\times$  sites occurrence matrix. The sum of each row is the abundance of that species, if the number of individuals (or a measure of cover or biomass) found at each site has been recorded; otherwise, if only the presence or absence of the species has been recorded, it is the range of the species within the area sampled. Surveys thus lead to two related questions about the ecological characteristics of species. The first is to explain the variation in abundance or range among species. The second is to explain why the range of a species includes some sites and not others. Five kinds of hypothesis, of different levels of complexity, have been put forward to answer these questions.

1 *The random model.* The simplest hypothesis is that distribution and abundance are determined by chance alone: each individual, anywhere within the area sampled, belongs to a given species with a fixed probability. Species are thus distributed at random among sites, and range or abundance follow a Poisson distribution.

2 *The neutral model.* In practice, however, it has been found that most species are not randomly distributed, but are instead patchy or aggregated. The simplest hypothesis to explain aggregation is that it arises through local dispersal alone, without any systematic differentiation among species or sites. The observed pattern is then the outcome of chance plus history. This situation is represented by a neutral community model, or NCM (Bell 2000).

3 *The ecological model.* A patchy distribution may arise from a spatial NCM, but need not necessarily do so. It might instead arise from a patchy distribution of resource input, so that sites differ in productivity. Some sites may then support many more individuals, and thereby many more species, than others. The observed patterns are then caused by chance plus history plus environmental variance.

4 *The evolutionary model.* When the environment is heterogeneous, lineages will tend to become adapted to local conditions of growth. Observed patterns will then

\* Biology Department, McGill University, 1205 Ave Dr Penfield, Montreal, Quebec, Canada H3A 1B1,

† Redpath Museum, McGill University, 859 Sherbrooke St West, Montreal, Quebec, Canada H3K 1B6

and ‡ Department of Plant Sciences, Macdonald Campus, McGill University, Lakeshore Boulevard, Ste-Anne-de-Bellevue, Quebec, Canada H9X 3V9.

be caused by chance plus history plus environmental variance plus selection. The distribution of a species will then depend in part on the distribution of the particular factor or combination of factors to which it is adapted.

**5 *The coevolutionary model.*** The growth of a species at a site may itself change the characteristics of that site. This will be true for any depletable resource, and there may be complex interactions, involving continual mutual adaptation and counter-adaptation, among antagonists such as predators and prey. In any case, the distribution of a species is constrained by the distributions of others.

In this chapter we are primarily concerned to evaluate the evolutionary model: to what extent do distributions reflect local adaptation in heterogeneous environments? Local adaptation is caused by selection within local populations that favours individuals with high fitness over some relatively narrow range of conditions of growth. Divergent selection causes species to be locally adapted to different conditions of growth. When a landscape is occupied by a species, through dispersal, it will tend to flourish at sites which provide the conditions of growth to which it has in the past become locally adapted, whereas it will often fail to become established at sites to which it is not well adapted. Because species have become adapted to different kinds of site, the continued dispersal of a group of species into a region will lead to distributions that are to some extent segregated from one another. This can be called selection, or sorting, or competition, or community assembly; these terms all refer to the process whereby observed patterns of distribution are generated by differential success over sites, itself the consequence of previous natural selection acting within populations. The restriction of a species to certain kinds of site is thus a consequence of local adaptation. Moreover, the degree of specialization displayed by a species, that is, the narrowness of the range of sites in which it is found, will reflect the degree of local adaptation. These are the main propositions that we shall examine in this paper.

## **Evidence from experiments and surveys**

### **Identification of local adaptation by transplant experiments**

The evolutionary model is tested directly by experiments in which families whose provenance is known are grown in different sites where their performance is measured. 'Performance' is ideally the same as 'fitness'; in practice, a complete seed-to-seed measure of increase is difficult to obtain, and in most cases some component of fitness, such as ramet survival or seed set, which we refer to generically as performance, is used instead. When plants are transferred between sites that have experienced different kinds of artificial disturbance, there is often unmistakable evidence of divergent specialization (e.g. explant studies by Jain and Bradshaw (1966), or reciprocal transplant studies by Davies and Snaydon (1976)). Transplant experiments involving natural communities also tend to demonstrate local adaptation quite readily, provided that they are conducted on sufficiently large geographical

scales. This was the object of the extensive common garden trials set up early in the 20th century (see Hiesey 1940). Reciprocal transplants involving seminatural sites several hundred kilometres apart often show that residents are consistently superior to incomers for at least some components of fitness (Antonovics & Primack 1982; Schmidt & Levin 1988; Jordan 1992). The same effect has sometimes been found at much smaller scales of 100 m or less, for example between grassland and woodland sites (Antonovics 1976; Lovett Doust 1981). A related observation is that the fitness of a family may decrease with distance from the parental site (Schmitt & Gamble 1990). Other experiments conducted over small distances, however, have failed to demonstrate any consistent superiority of residents (Cheplick 1988; van Tienderen & van der Toorn 1991). In brief, there is considerable experimental evidence for local adaptation, especially at rather large spatial scales.

### Biological surveys

Surveys are much easier to do than experiments, so we often know the occurrence of species among sites but not their performance. It may be possible, nevertheless, to demonstrate local adaptation. The reason is that the response of species to sites is presumed to be caused by the ecological characteristics of those sites, so that if we can demonstrate a correlation between the abundance of a species and the level of some environmental factor, then this is evidence for local adaptation, subject to the condition of repeatability described below. Unfortunately, it is not possible to use biological surveys to *falsify* a general hypothesis of local adaptation, for the simple reason that imagination cannot be relied on to identify the factor to which species are adapted. The best that can be done with survey data alone is to guess which factor may be responsible for shaping a given species distribution, and then test the specific hypothesis of local adaptation with respect to this factor. The first problem raised by this approach, then, is how to make this guess.

The approach that we have followed is to take overall productivity as the first-order environmental factor (or, more precisely, as reflecting the underlying environmental factor or factors that most strongly influence plant growth); then to consider the known components of overall productivity; and only then to speculate about the idiosyncratic responses of particular species. Productivity is determined primarily by nutrient concentrations, and secondarily by factors which influence the rate of nutrient utilization, such as radiant flux, water availability and pH. These can be measured on the ground, or, failing that, inferred from maps of topography, climate or geology.

### Measurement of local adaptation from survey data

The consequence of local adaptation apparent from survey data is that a species will occupy a restricted range of sites, relative to those available, with respect to a given environmental factor. The extent of local adaptation to a given factor is therefore appropriately measured by the variance of occupied sites as a fraction of the variance of all sites. To avoid the statistical shortcomings of proportions, and

to obtain a measure that increases as adaptation becomes more precise, we define precision as

$$\text{Precision} = -\log(s_{\text{occ}}^2/s_{\text{all}}^2) \quad (1)$$

where  $s_{\text{occ}}^2$  and  $s_{\text{all}}^2$  are the variances of occupied sites alone and of all sites, respectively.

The consequences of local adaptation for diversity and abundance depend not only on adaptation, but on divergent adaptation. The extent of divergence is measured by the variance of the mean values of occupied sites among a set of species. We shall use the standardized difference from the environmental mean as a measure that can be used to compare the response to different environmental factors:

$$\text{Eccentricity} = (m_{\text{occ}} - m_{\text{all}})/s_{\text{all}} \quad (2)$$

Where  $m_{\text{occ}}$  and  $m_{\text{all}}$  are the mean values of occupied sites alone and of all sites, respectively. Divergence is then defined as the variance of eccentricity.

We can then formulate the question that we began with: To what extent do distributions reflect local adaptation in heterogeneous environments? In a more quantitative way as: What are the average values of precision and divergence, and how do they vary among taxa and among environmental factors?

### General theory of adaptation in relation to ecological scale

The general answer to this question is, that it depends on the scale of the investigation. Any survey will involve a particular environmental scale, the size of the region surveyed and of the sites within it, and a particular phylogenetic scale, the relatedness of the organisms recorded. The interpretation of the survey is sensitive to both.

Consider first the environment, where the issue is whether sites within a region are occupied by different species as the consequence of local adaptation. The precision of adaptation will depend principally on the balance between selection and immigration. In a small region, the number of immigrants will be large relative to the number of births within the site, whereas in large regions the converse is likely to be the case. At a scale of 1 m, the pattern of vegetation is caused largely by the accidents of colonization, although adaptation to factors such as microtopographical relief may sometimes occur. At a scale of 1 km, the much greater variance of physical factors such as soil moisture and light leads to distributions that are restricted to (say) bogs or dry forest, although most species may be capable of growing at most sites. At a scale of a 1000 km, major differences in climate and geology are likely to occur, and almost all species will be restricted to a small fraction of sites.

Organisms do not measure their environment in units of metres, of course: they measure it in units of themselves. More precisely, their response to environmental heterogeneity will depend on two natural scales: the individual scale of the growth of single organisms, and the dispersal scale of the propagules they release. These will both be enormously different for, say, an alga and an aspen, so that any conclusions about scale and adaptation must take the organisms concerned into account. As a

crude rule of thumb, we might expect local adaptation to be much more conspicuous within regions exceeding the dispersal scale than in smaller regions.

A second general rule applies to the organisms included in a survey: lineages are more likely to become distinctively specialized if they are only distantly related. The minimal genetic change, a single-base substitution, is likely to be neutral or nearly so; in all events, it is unlikely to give rise to two lines adapted to different conditions of growth. At the other extreme, lineages that have diverged very widely, such as a fern and a sedge, are almost certain to have accumulated a variety of substantial ecological differences. There are exceptions to both of these statements: single mutations do occasionally produce ecological differentiation, whereas organisms belonging to different phyla may share some specializations, at least, and occur together at the same sites. In general, however, the likelihood that two lineages will have evolved distinctive local adaptations increases with the genetic distance between them.

Putting these two rules together, we are led to the generalization that distinctive local adaptation is more likely to evolve as the environmental variation within the survey region increases, and as genetic variation among the organisms surveyed increases (see Kassen & Bell 2000). It synthesizes a number of ideas that have long been current in community ecology and population genetics, in particular community turnover (Whittaker 1970) and limiting similarity (see Hubbell & Foster 1986). In doing so, it makes it clear that the most pervasive generalizations that can be made about local adaptation, and thus about the diversity of sites and the abundance of species, hinge on concepts of scale.

## The biological survey of Mont St-Hilaire

### The survey

Biological surveys are the basis for all of our knowledge about the distribution and abundance of organisms, and therefore about the extent of local adaptation. Most published surveys are of little use because they were not conducted systematically; survey data can be interpreted only when all sites have been searched for all species with the same effort and using the same procedures. A few surveys, although unsystematic, are nearly exhaustive, after the records of generations of naturalists have accumulated, and these are perhaps the best available sources of information. All of them, however, exemplify the 'survey paradox'. We wish to use survey data to evaluate hypotheses about the natural processes that shape distribution and abundance, and must therefore conduct the survey in regions that have not been severely disturbed by recent human activity. Unfortunately, all the most rigorous and comprehensive surveys have been conducted in countries such as Britain, Germany and the Netherlands, where the landscape is almost completely humanized. The survey paradox is that where we have adequate data it cannot be used, and where we require data it is not available.

We are conducting a systematic biological survey of a large surviving fragment of

old-growth forest in the St Lawrence valley in defiance of this paradox. The site is Mont St-Hilaire, an isolated hill some 1000 ha in extent, where the forest has never been cleared (see Maycock 1961). Most of the area is beech–maple forest characteristic of the region, with scattered oak and pine. Teams of trained recorders search each hectare for a given group of plants, following a fixed pattern. The groups for which we have complete information to date are ferns, sedges and trees, giving us consistent estimates of the distribution of a total of 125 species. Sedges form a group of closely related species within a single genus, *Carex*; ferns and trees are more diverse taxa. The survey thus encompasses groups of different phylogenetic extent within a region consisting chiefly of a single ‘habitat’.

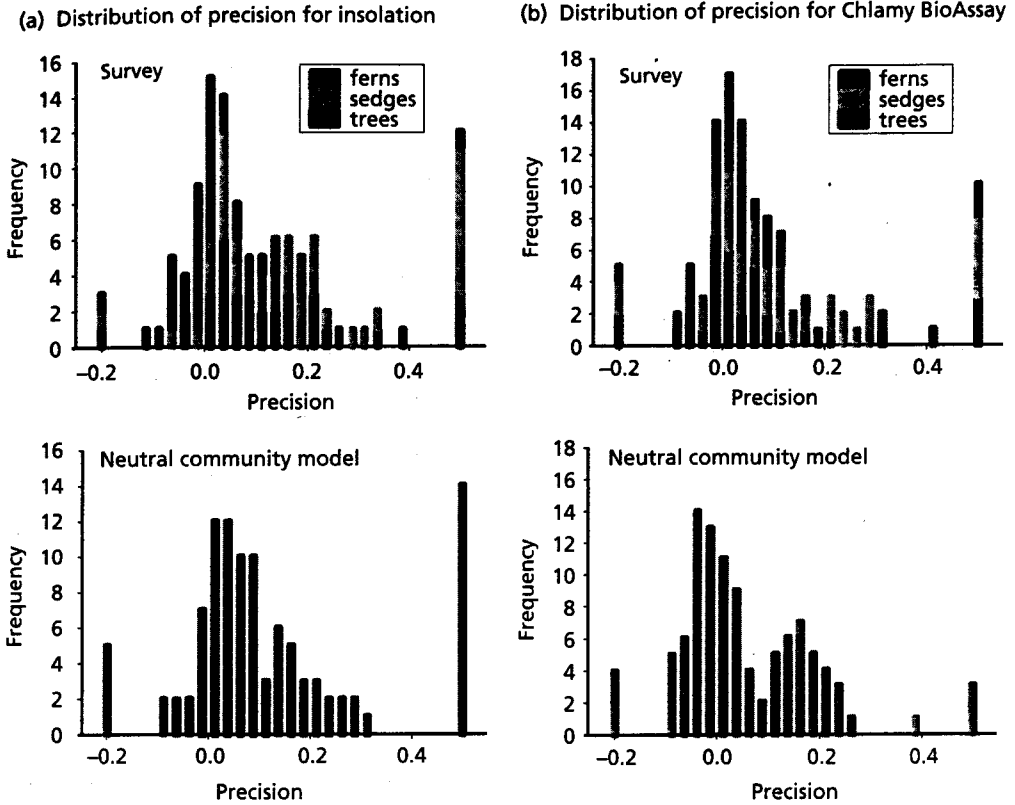
Data on landscape structure comes in part from topography and in part from extensive explant trials. The digital elevation model for the area yields estimates of elevation, slope, water flow and insolation for each 5 m × 5 m cell, which for the purposes of this analysis are used to obtain averages for each hectare. Soil samples were collected for each hectare. We measured pH and the production of three organisms: the chlorophyte *Chlamydomonas* and the sedges *Carex arctata* and *Carex prasina*. These procedures and the spatial structure of the eight components of productivity are described by G. Bell, M. Lechowicz and M. J. Waterway (unpublished). Briefly, the spatial structure of a given environmental factor can be characterized by the slope of the regression of log variance on log distance for all pairwise combinations of samples (Bell *et al.* 1993). A steep slope indicates a coarse-grained environment (with respect to the particular factor analysed), and a shallow slope a fine-grained environment. Our soil measures all have shallow slopes of about 0.1, indicating that there is a great deal of environmental variance within each hectare, below the grain of our plant survey. We are, of course, unable to identify any correlation between occurrence and environmental state at scales below the grain of the survey; these are the subject of further research (e.g. Richard *et al.* 2000).

### Precision

The distribution of precision for two representative factors, insolation and *Chlamydomonas* production, are shown in Figure 6.1. They resemble left-skewed log-normal with a mode at small positive values. The overall mean for all eight factors was +0.0845, corresponding to 82% of the overall environmental variance. Thus, most species occupy a large fraction of the available range of growth conditions. Errors of estimation give rise to modest negative values, whereas the long tail to the right consists of progressively more specialized species.

Analysis of covariance shows that overall range has a strong effect on precision (Table 6.1). The relationship is triangular (Figure 6.2). Very widespread species that occupy a large fraction of sites are constrained to have precision of close to zero. In progressively less abundant species the range of precision extends to more positive values, reaching about +1 (10% of environmental variance) for species occupying 10 sites (1% of total area). Thus, although rare species may have any degree of specialization, the most specialized species are always rare.

Precision also varies among groups of organisms and among environmental



**Figure 6.1** Frequency distribution of precision of local adaptation, in the Mont St-Hilaire survey and in the neutral community model (NCM). (a) Insolation; (b) *Chlamydomonas* bioassay.

factors (Figure 6.3). In almost all cases, the herbaceous plants, ferns and sedges have greater precision than trees. Some environmental factors (such as elevation and insolation) are associated with greater precision than others (such as water flow), but no more general pattern is apparent.

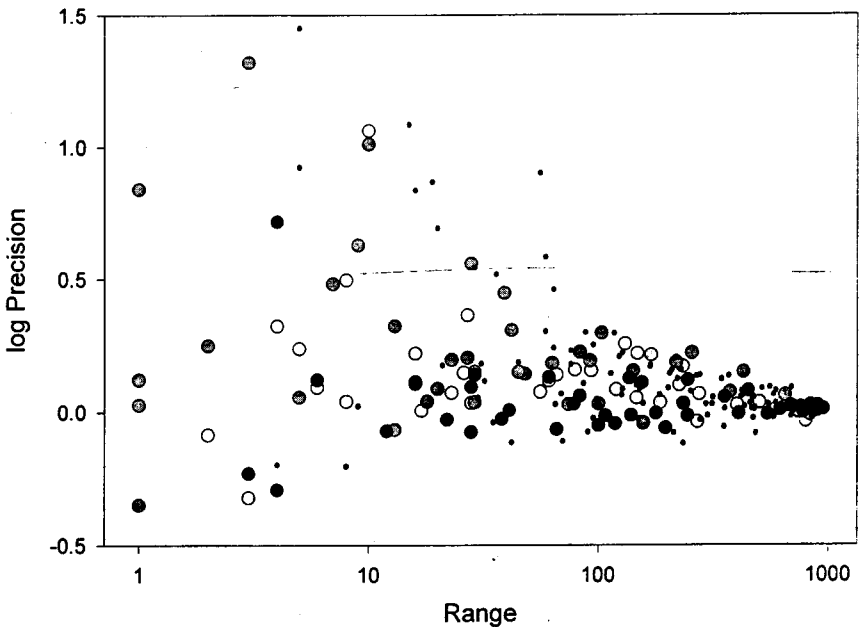
Precision is expected to vary with scale. If sites are agglomerated into progressively larger blocks, precision should increase with block size as selection becomes more effective. We found, however, that precision fluctuated with block size without any evident trend (Figure 6.4).

**Eccentricity**

Over all species, eccentricity is approximately normally distributed around zero (Figure 6.5). This is the outcome, however, of summing groups whose distributions may be skewed. Ferns are skewed towards negative values for insolation, for instance, whereas sedges are skewed towards positive values.

**Table 6.1** Analysis of covariance of precision of adaptation. The continuous variate is range (number of hectares occupied by species). Factor is a categorical variable, representing the eight environmental factors whose spatial structure was measured. For the survey data, species were placed into one of four monophyletic groups: ferns, sedges, conifers and woody dicots. Variation among species within groups supplies the common error term.

| Source                                      | d.f. | MS     | F    | P       |
|---|------|--------|------|---------|
| <i>Biological survey of Mont St-Hilaire</i> |      |        |      |         |
| Range                                       | 1    | 2.3655 | 23.5 | <0.0001 |
| Group                                       | 3    | 0.2750 | 2.73 | 0.043   |
| Factor                                      | 7    | 0.2960 | 2.94 | 0.005   |
| Group x factor                              | 21   | 0.0777 | <1   |         |
| Species (group)                             | 911  | 0.1006 |      |         |
| <i>Spatial neutral community model</i>      |      |        |      |         |
| Range                                       | 1    | 2.1534 | 51.4 | <0.0001 |
| Factor                                      | 7    | 0.3781 | 9.03 | <0.0001 |
| Species                                     | 815  | 0.0419 |      |         |



**Figure 6.2** Relationship between precision and range for insolation. Symbols are: open circles, ferns; lightly shaded circles, coniferous trees; medium shaded circles, sedges; solid circles, broad-leaved trees; dots, neutral community model.

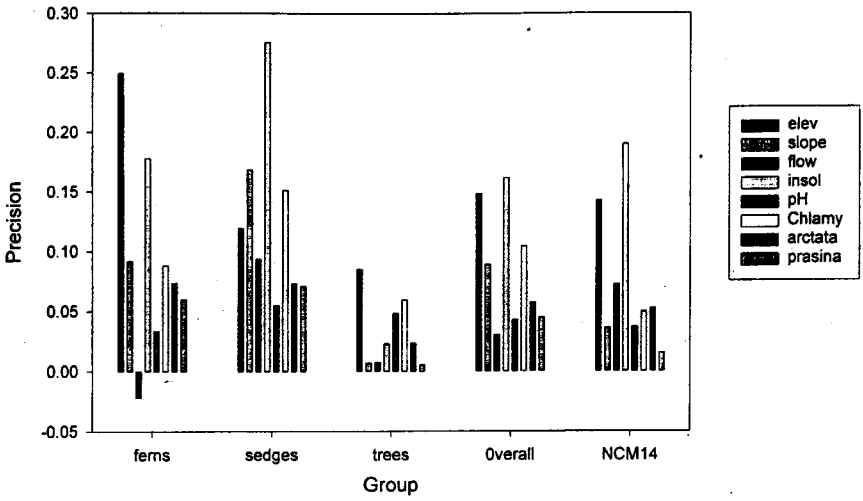


Figure 6.3 The precision of adaptation for different groups and environmental factors, in survey data and the neutral community model (NCM)

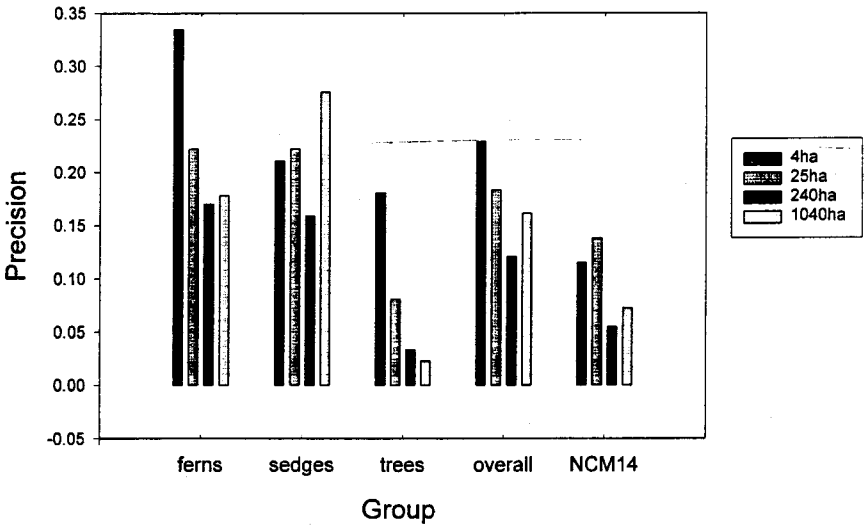
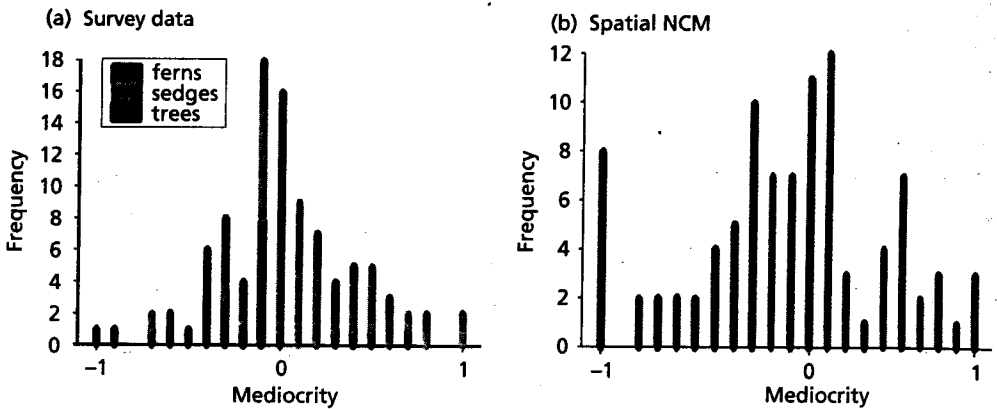


Figure 6.4 The precision of adaptation to insolation in relation to spatial scale, in the survey and the neutral community model (NCM)



**Figure 6.5** The distribution of eccentricity for insolation, in the survey and the neutral community model (NCM)

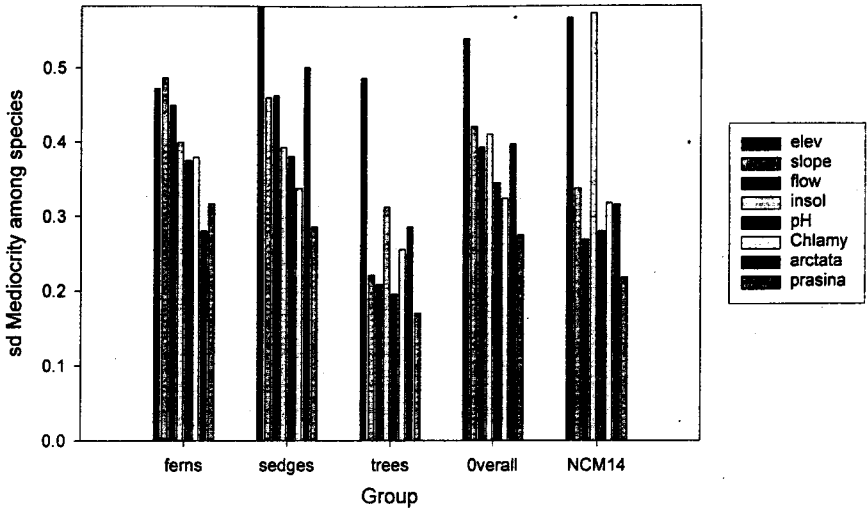
The average value of divergence was 0.41, so that somewhat more than 95% of species occupied sites with average values within 1 s.d. of the overall environmental mean (Figure 6.5). The extent of divergence varied among groups and among environmental factors (Figure 6.6). For most (14/16) comparisons, ferns and sedges have diverged more than trees. There is also a tendency, although not a very strong one, for divergence to be more marked for the factors related to topography than for those related to soil conditions.

In short, the survey shows that most species are specialized to some extent, with respect to any component of productivity; that high degrees of specialization are found predominantly among rare species; and that precision and divergence vary among groups and among environmental factors. We could now proceed to interpret these patterns in terms of the natural history of each species, investigating the extent to which each is restricted to a narrow range of conditions, and attempting to identify the physiological basis of each case of local adaptation. We shall instead ask first whether the patterns require any biological interpretation at all in terms of local adaptation, or whether they might arise instead through some simpler process.

## Neutral community models

### The spatially located NCM

The patterns emerging from the survey are clearly non-random, and the random model can be dismissed at once. It is not so easy to dismiss the neutral model, in which pattern arises solely through limited local dispersal without any ecological differences among individuals whatsoever. In order to investigate this possibility, we need to construct a neutral simulacrum of the survey, using the same number of



**Figure 6.6** The magnitude of divergence (variance of eccentricity) in the survey and the neutral community model (NCM).

species in the same area, so that we can compare the output of the model directly with the analysis of the survey itself.

At a single site, an NCM can be constructed for a community comprising a fixed number of species by assuming that the rates of birth, death and immigration are identical for all species. This leads to a distribution of abundance among species that resembles a log-normal curve, skewed to the left by immigration; at the limit where immigration greatly exceeds birth, this approaches a log-series distribution (Bell 2000). This has been shown to represent a new distribution, the 'zero-sum multinomial' by Hubbell (Chapter 18 and Hubbell 2001). To represent processes within the region where a survey has been conducted, a spatial neutral model can be constructed by placing an NCM at each site on a lattice. Founding individuals are assigned to sites at random, so that the community is initially described by the random model. When an individual reproduces, however, its offspring may disperse away from the natal site. This can be simulated by a random walk: with fixed probability the newborn individual moves to one of the four adjacent sites that can be reached by a rook's move. Once there, it again moves, with the same probability, and so forth, until the condition for movement is not met, when it settles in the site it last occupied. Individuals that are born close to the edge of the region may stray over the edge and are then lost to the community; this loss is balanced by new immigration from an external source into the marginal sites. If the probability of movement is very low, most newborns will settle in their natal site, whereas if it is high they will become more or

less widely dispersed away from it. In this way, a correlation between nearby sites is created, and the initially random distribution becomes more or less aggregated.

To create a simulated survey, founding individuals belonging to 125 species were settled at random on a  $50 \times 50$  lattice and allowed to propagate for 2000 cycles. A piece shaped exactly like the hectare survey grid at Mont St-Hilaire was cut out of the centre of the lattice, avoiding any edge effects caused by immigration. The distributions of the species generated by the model within this region are then used to compute precision and divergence, using the observed spatial structure of the environmental factors. Comparing this output with the survey results is not a statistical test, however. To run the NCM requires specifying five parameters—birth rate, death rate, dispersal probability, immigration rate and carrying capacity per site—all of which are unknown. They will be unknown for almost any conceivable survey. We are necessarily restricted to asking whether the patterns that emerge from the NCM are qualitatively similar to survey data.

The NCM readily generates species distributions that look uncannily like the results of real surveys, with great variation in range or overall abundance among species. Within a site, the distribution of abundance among species resembles a skewed log-normal, as found previously for isolated communities (Bell 2000). We have extended this result by finding that the distribution of both overall abundance and range among species within a region comprising many sites that exchange migrants resembles a geometric or log-series distribution, as predicted by Hubbell (2001). The model output depends in detail on parameter values. We chose parameter values that led to a distribution of range similar to that found in the survey, with a broad band of species at intermediate abundance. Specifically, we assigned a birth rate very slightly higher than the death rate ( $b = 0.505$ ,  $d = 0.500$  per individual per cycle), to counter the leakage of dispersing offspring across the edge of the lattice; a low immigration rate ( $m = 0.00025$  per species per marginal cell) to forestall species extinctions; a moderate dispersal rate for offspring ( $s = 0.1$ ); and a carrying capacity of 500 individuals per site, which eventually results in a total population of about half a million individuals on the Mont St-Hilaire cut-out. We have restricted our comparison to a single realization of this parameter set. Different realizations produce similar results. Changing the parameters can cause substantial changes in the distribution of range, but our results seem broadly applicable to moderate dispersal probabilities of 0.05–0.5 or so.

### Patterns in neutral communities

The basic properties of the model were as follows. The distribution of precision is left-skewed log-normal, with a mode at small negative values (see Figure 6.1). The overall mean precision was +0.0742, corresponding to 84% of the environmental variance. Abundance has a highly significant effect on precision (see Table 6.1). The relationship is again triangular, with high degrees of specialization being restricted to rare species (see Figure 6.2). Species cannot be assigned to groups in this model, but precision varies among environmental factors (see Table 6.1). Elevation and insolation are associated with the greatest negative values of average precision (see

Figure 6.3). There is no consistent relationship between precision and block size (see Figure 6.4). Eccentricity was more or less normally distributed about zero (see Figure 6.5), with an average value of divergence over all factors of 0.3855. The degree of divergence varied among factors, the greatest values being associated with topographically derived variables (see Figure 6.6).

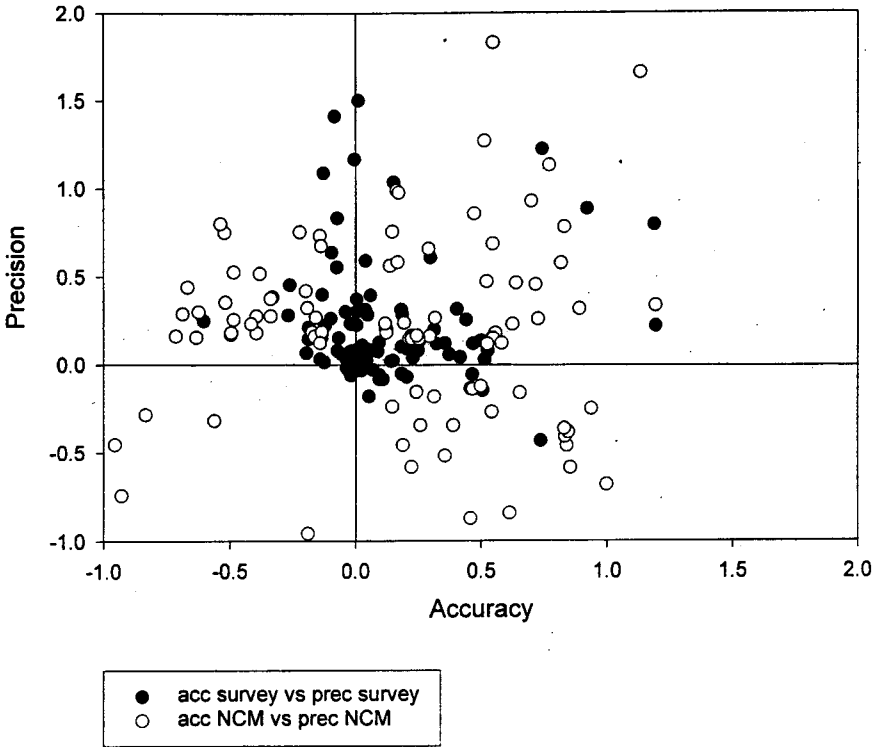
In short, the NCM-generated patterns that are strikingly similar to the survey. No attempt was made to study the whole parameter space of the model, so it would be surprising if this conclusion applies only to a very narrow and unrealistic range of parameters. (It may well apply only to parameter sets that generate abundance and range distributions that approximate real data, however.) Much of our preceding analysis therefore not only fails to provide a measure of the extent of local adaptation, it fails even to demonstrate that any local adaptation has occurred.

### Accuracy

In the light of the NCM results, it is easy to appreciate that the weakness of the concept of precision is that no value of this statistic, however large, can be interpreted as evidence for local adaptation. Suppose that a species were to arrive at some site by chance, grow there and in time disperse to a group of nearby sites. These sites are likely to be similar, because of their proximity, and will therefore represent only a small part of the regional variance. The species would thus be judged to be locally adapted, whereas it is in fact merely locally dispersed. The hallmark of local adaptation is not that it causes a restricted pattern of distribution, but that it repeatedly causes the same pattern. It can be demonstrated from survey data, therefore, only by aggregating neighbouring sites into blocks, and showing not only that occupied sites have low variance but also that they have a similar mean throughout the region surveyed. More formally, suppose that having partitioned the region into blocks of neighbouring sites, we estimate the variances among sites within blocks,  $s^2_{\text{within,all}}$ , and among blocks,  $s^2_{\text{among,all}}$ . Furthermore, we estimate the corresponding variances for the sites occupied by a given species,  $s^2_{\text{within,occ}}$  and  $s^2_{\text{among,occ}}$ . These estimates can then be used to derive two measures of local adaptation.

- 1 The precision of adaptation is the within-block variance of occupied sites, normalized by the overall within-block variance: it is expressed as  $\text{precision} = -\log(s^2_{\text{within,occ}} / s^2_{\text{within,all}})$ , so that greater values indicate more precise adaptation.
- 2 The accuracy of adaptation is the among-block variance of occupied sites, normalized by the overall among-block variance:  $\text{accuracy} = -\log(s^2_{\text{among,occ}} / s^2_{\text{among,all}})$ .

This provides a method of distinguishing between local adaptation and neutral processes. In practice, it should be applied only to blocks of moderate size that provide adequate degrees of freedom for estimating both within-block and among-block variance components. Figure 6.7 shows the results of a plot of precision on accuracy for 25-ha blocks. Many apparently high-precision species turn out to have low accuracy, making it difficult to interpret their restricted range of occurrence as being caused by selection. It is true that the NCM results show somewhat lower accuracy than the survey, but the cloud of points produced by the NCM overlaps so



**Figure 6.7** Precision and accuracy of local adaptation in the survey and the neutral community model (NCM)

broadly with the survey that it is difficult to argue that the analysis strengthens the case for local adaptation. This conclusion applies to all block sizes between 4 ha and 240 ha.

**The experimental evidence**

Extensive implant experiments carried out at Mont St Hilaire have been reported in a previous paper (Bell *et al.* 2000). They involved setting out several thousand ramets of 15 species of *Carex* along 3 km of transects within the forest. The overall survival of ramets in the first year showed that most sites in the forest would support growth. The habitat requirements of these species are therefore quite broad, and as most forest sedges usually grow as spaced plants, which are unlikely to compete directly with one another, they are unlikely to express precise or divergent adaptation. The rate of survival, moreover, was not correlated with range or abundance; indeed, the most successful species in these implant trials was *Carex bromoides*, which

ranked only 31st in range of the 45 species found in the survey. It may be that establishment is more sensitive to germination than to the survival of large ramets. We now know, however, that the species with the most rapid and consistent germination of fresh seed is *Carex prasina* (unpublished data), again a rather uncommon species which ranked 21st in the survey. Furthermore, we have conducted targeted implant experiments which failed to show any tendency for ramets to survive better when planted close to a resident plant of the same species (Bell *et al.* 2001).

The explant experiments allow us to compare the growth of *Carex arctata* and *Carex prasina* in soil samples from sites where they were present with growth in samples from sites where they did not occur. The two species have contrasting ranges: *Carex prasina* was found in only 4% of sites, whereas *Carex arctata* is the third most abundant sedge in the forest, and was found at 74% of sites. The mean dry weight of *Carex arctata* grown in soil from sites from which the species was recorded was 73.5 mg (s.e. 0.9 mg) and in unoccupied sites was 74.9 mg (s.e. 1.8 mg). The dry weight of *Carex prasina* for occupied sites was 72.5 mg (s.e. 5.6 mg) and for unoccupied sites was 81.4 mg (s.e. 1.1 mg). There is no evidence that either species is specialized to the soil of its neighbourhood.

Both implant and explant experiments are consistent with a neutralist interpretation of distribution for sedges within the forest.

### The comparative evidence

It might be argued that our failure to detect the local adaptation that is well known to be characteristic of many plants is simply because our data are unreliable. This is not the case. The biological survey and the environmental mapping that we have conducted are among the most systematic and comprehensive on record. When particular species are isolated, they usually have the expected properties. Bracken fern (*Pteridium aquilinum*), for example, is well known to grow chiefly in open sunny areas. When its distribution is analysed against insolation, it has an eccentricity of +0.57 and a precision of +0.21, while at a block size of 25 ha its accuracy is +0.37. It therefore appears on Figure 6.7 as one of the minority of species with a combination of precision and accuracy. This is an exceptional case; most species are not as clearly specialized. Our analysis does not refute the existence of conventional patterns of local adaptation, however. Indeed, the difference in eccentricity among groups is the clearest signal of local adaptation to emerge from our data. Rather, it refutes the possibility that the average or ensemble properties of species distributions can be used directly to demonstrate the existence of local adaptation or to estimate its precision.

### Model structure

It is easy to specify parameter values such that the NCM would not generate patterns resembling survey data. If the probability of local dispersal is set to zero, for example, the distributions set up by initial colonization are retained indefinitely; at the other extreme, if offspring are nearly certain to disperse they settle almost at random, after a very long sequence of moves from site to site. Moderate levels of dispersal, however, always generate survey-like patterns. Nevertheless, many correspondents and

reviewers have argued that a five-parameter model can be tuned to produce almost any result, and that the qualitative correspondence between the survey results and the NCM output cannot be taken as support for a neutral interpretation of species distributions and the associated phenomena of diversity and abundance. We answer as follows. In the first place, *all community models have the same number of parameters*. They differ only in the number that may be varied. A model of simple exponential growth may appear to have only a single parameter, but this is because all other parameters (the rate of immigration, for example) have been set to some fixed value (zero, in this case), so that they do not appear in the presentation of the model. This approach was necessary before the advent of high-speed computing made it possible to study individual-based, equation-free community models, and it remains a useful heuristic device, but its simplicity is apparent rather than real. Secondly, if the number of variable parameters is the criterion, neutral models are necessarily simpler than any theory of local adaptation, which will require many additional, explicitly defined values for site-specific fitness. Finally, we do not claim that the patterns we have found provide decisive evidence for a neutral interpretation of communities, although we do claim that these patterns cannot henceforth be used as evidence for any non-neutral interpretation. More precisely: when the grain and extent of a surveyed area are such that there are moderate rates of local dispersal between adjacent sites, the spatial structure of species composition will not reflect local adaptation.

### Grain and extent

The actual level of dispersal achieved by plants will depend in part on the nature of the propagules they produce, but it will also depend on the design of the survey or the blocking of the data: dispersal will be low when grain is large, regardless of extent, but high when both grain and extent are small. The prominence of local adaptation in the structure of communities is likely to depend on the grain and extent at which the region concerned is surveyed or analysed. Our conclusions, therefore, apply only to the scale of the survey that we have used, with a grain of 1 ha and an extent of about 1000 ha. We expect that a more extensive survey should display more pronounced local adaptation, because larger areas will contain more environmental variance. In practice, however, this may not necessarily be the case. The most authoritative published surveys, such as the grid-based surveys of European regions and the county-based surveys of the USA, all comprise similar numbers of sites, from several hundreds to a few thousands. This is because there is a correlation between grain and extent: more extensive surveys have coarser grain. A survey of, say,  $10^6$  ha with a grain of 1 ha might well provide much more evidence of local adaptation than we have been able to document within  $10^3$  ha. No such survey exists, however, and none well ever be carried out. The *Atlas Florae Europaeae* (Jalas & Suominen 1972) deals with an area of about  $10^9$  ha, at a grain size of  $2.5 \times 10^5$  ha; the *Atlas of the British Flora* (Perring & Walters 1962), an area of about  $2.5 \times 10^7$  ha at a grain size of  $10^4$  ha; the best available British county atlases, such as that for the Leicestershire flora (Primavesi & Evans 1988), an area of about  $1.5 \times 10^5$  ha at a grain size of  $4 \times 10^2$  ha. These surveys therefore offer increased among-site variance, but at the expense of

increased within-site variance. Just as adaptation cannot be detected at scales greater than the extent of a survey, neither can it be detected at scales less than the grain of a survey. The best available data may therefore be too coarse to reveal local adaptation, quite apart from referring to developed landscapes. The only satisfactory solution to this quandary is an extensive, fine-grained survey of a remote wilderness, and no such survey has yet been attempted.

### Neutral macroecology

It might also be urged that real communities possess distinctive properties that are unlikely to be exhibited by neutral models. Species tend to be consistently abundant or rare, for example, when quite independent localities within the same region are sampled; thus, if we were to sample another Monteregian forest we would probably find that *Carex arctata* was much more abundant than *Carex prasina*, as it is at Mont St-Hilaire. This constitutes indirect evidence for local adaptation, in so far as it is consistent with the conclusion that some species are systematically more specialized than others. It is equally consistent with a neutral model, however. When the abundance of species at occupied sites is analysed for the NCM, the variance within sites is 56.7 and the variance among sites 301.6, yielding an intraclass correlation of 0.84. There is a pronounced tendency for some species to be locally abundant everywhere whereas others are locally scarce everywhere. The distribution of abundance among species at a site often resembles a left-skewed log-normal, whereas the distribution of range for the whole region is often more or less geometrical; both are properties of the NCM. It is also often found that local abundance is correlated with range, and this relationship has been held to demonstrate patterns of specialization (see Gaston 1996). This is likewise a feature of the NCM, however, where the regression of mean local abundance on range (both log-transformed) for the 125 species of the model was +0.37, with  $r^2 = 0.74$ .

The fact that a simple neutral model can generate spatial patterns resembling survey data has broad implications for community ecology (see also Chapter 18 and Hubbell 2001). Species diversity is thought to depend on the extent of local adaptation, and if neutral models mirror patterns of local adaptation then they will also mirror patterns of diversity. They will readily generate a species–area curve, for instance, or the relationship between diversity and environmental heterogeneity. Most theories of range and abundance also invoke the degree of specialization as the key attribute of species. Our results show that the use of survey data to evaluate theories of any kind about the diversity of sites or the abundance of organisms is likely to be completely misleading in the absence of an appropriate NCM.

### Summary

The distribution of species is often explained in terms of divergent specialization: having become adapted in the past to particular conditions of growth, species are now found predominantly in sites that provide these conditions, so that there is a close fit between the composition of the community and the state of the environ-

ment. The major patterns of diversity and abundance that follow from species distributions can then be interpreted in terms of local adaptation. An alternative view is that all species have identical demographic properties, and that patterns of distribution, diversity and abundance arise solely as the consequence of local dispersal. We present the results of a detailed physical and biological survey of plants in an old-growth forest, and use them to calculate the degree of local adaptation in terms of the environmental variance of sites occupied by a species as a fraction of the overall variance among sites. We compare the outcome with a parallel analysis of the spatial patterns generated by a neutral community model (NCM). The patterns observed in the forest are qualitatively similar to those generated by the NCM. It is concluded that there is no evidence for community structure generated by local adaptation at the grain (1 ha) and extent (1000 ha) of our survey. Furthermore, we argue that fundamental ecological patterns such as the species–area and range–abundance relationships cannot be interpreted reliably except in the context of an appropriate NCM.

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