10

Spatial diversity analysis

Introduction

The topic of diversity in biological systems, whether called 'species diversity', 'ecological diversity', 'biological diversity', or just 'biodiversity', is the topic of literally thousands of scientific articles and is included as a central concept, sometimes the main subject, of many books (Huston 1994; Magurran 2004; Rosenzweig 1995; Sarkar 2009; Magurran & McGill 2010). Informally, diversity is related to the variety of classes or categories represented in a collection of objects. The concept comes up in a number of different areas for biological research including genetics, systematics and evolution, conservation biology, and ecology. Biological diversity in ecological systems is a concept of intense interest and of great theoretical as well as practical importance, which has implications for the coexistence of species and the structure of natural communities as well as for the persistence of species in disturbed systems, the conservation of organisms, and the functioning of the systems in which they occur.

In the ecological literature, much of the discussion of diversity has dealt with what the concept means, or should mean, and how the characteristic is, or should be, measured. Diversity thus includes several aspects which make its discussion complex. As early as 1971, Hurlbert wrote a paper on the 'nonconcept' of species diversity, suggesting that the idea had been so abused as to become meaningless and that the term should be abandoned. More recently, Huston (1994, p. 64) commented that 'Far too much attention has been paid to comparison and criticism of *statistical* methods for quantifying diversity'. We will try to bring clarity to those parts of the discussion needed for spatial diversity analysis, but it is worth remembering Colwell's recent reminder that the concept of diversity is "a human construct without any unique mathematical meaning" (Colwell 2009). Our own version of the same warning is that even richness, as one aspect of diversity, is a synthetic variable, and we will return to the implications of this fact within a spatial context.

Diversity is a measure of the unpredictability of the 'species' to which a randomly encountered 'individual' belongs. For example, Simpson's diversity index (given below as Eq. (10.1)) is the probability that two randomly chosen individuals from a community belong to different species. *Spatial diversity* is a measure of the unpredictability of the 'species' to which a randomly encountered 'individual' belongs, given the species of the individual last encountered in a spatial series of such encounters, or given the location of the encounter. This insight offers the choice of adapting the familiar non-spatial approaches to the study of diversity by including the locations of individuals or developing new measures designed specifically to include spatial information explicitly. To accomplish this we should begin with a discussion of the importance of spatial considerations in the study of diversity.

10.1 Space in diversity analysis

Diversity analysis requires tallying the species that are present at one location or in a given delimited area. As such, the basic treatment of diversity is 'aspatial'

and does not require any spatial component although space, as location or as scale, may be included; in fact, many discussions of diversity include some spatial aspects of the phenomenon, but they are often implicit rather than explicit. What may be most surprising is the extent to which the discussion of diversity has been clearly aspatial, not exclusively, but certainly overwhelmingly. At least some of the reason for that bias has to do with the organisms that are most frequently used for discussion and illustration of the topic: mobile animals such as birds, lizards, insects and fish are definite favourites. Of the nine worked examples in Magurran's book (2004), only one concerns plants; the others are fish (3), beetles (2), Lepidoptera, lizards and birds. In many instances, the opportunity for a spatial component in the analysis of diversity is limited by the data collection, often by the use of traps or sampling stations of some kind which gather the organisms from around them, at least partially erasing the natural pre-sampling spatial relationships among the individuals being identified and counted. Yet even mobile species occur in different proportions at different locations, so that a diversity measure can summarize implicitly various spatial components ranging from the location of the study, the study extent, and the change in the species list (turnover) between locations. It is also possible for a study of diversity to be based on a single undifferentiated collection from a single site and consisting of the abundances of species in a single classification. As the study extent increases, the number of species diversity (richness) also increases. This is the species–area curve effect that is well-known and well-studied (Figure 10.1*a*; Plotkin *et al.* 2000; Scheiner *et al.* 2000).

In this chapter, we wish to make the spatial aspect of the discussion of diversity explicit and clear because spatial analysis and diversity analysis intersect in several different ways. Most simply, we can ask how diversity, as usually conceived and measured, changes with location and how it is affected by the spatial structure of the environment in which the focal organisms occur. We can also ask how spatial locations and spatial structure can and should be included in the analysis of diversity. For example, we can ask whether fish communities are more diverse in northern lakes than in southern, in larger or smaller lakes, in more productive or less productive, and so on. Third is the question of how to carry out spatial analysis in order to elucidate the structure of diversity in natural systems.

If diversity itself is all about the unpredictability or predictability of the organisms we find, the spatial aspects of diversity are about the unpredictability of 'what' we find but also the unpredictability (or predictability) of 'where' we find them. There are at least four different ways in which spatial aspects of diversity can be included; some are not fully and explicitly spatial but only apparently or partially so, and there is a certain amount of overlap or confounding of the four categories. The four aspects that include space are

- spatial heterogeneity,
- location,
- scale, and
- propinquity and spatial dependence.

Let us examine these four with more detail.

10.1.1 Spatial heterogeneity

The effects of heterogeneity on diversity may be obvious in that a greater diversity of substrates, environmental conditions, or resources may support a greater diversity of species. Where that environmental heterogeneity itself has a spatial structure, it may translate into spatial structure for the biological diversity.

The expected heterogeneity among sites derives from a number of possible causes, including abiotic environmental factors, stochastic events such as colonization and extinction, and the oft-cited phenomenon of the decrease in ecological similarity with physical distance due to biological processes like dispersal (Nekola & White 1999; Soininen *et al.* 2007). The existence of such heterogeneity is acknowledged by the large literature on β-diversity (variation in species composition among sites, described below) in its various versions, whether as the gain or loss of species along an environmental gradient or as the among-site differences in species composition due to patchiness of underlying factors. Unless the position on gradients or the relative locations and distances of the sites are included in the analysis, this kind of study is not truly spatial because while it examines variability that exists

in space, it does not quantify that variability as a function of the embedding of the sample locations in a spatial context. To put this thought another way: the heterogeneity occurs in a spatial context but that context is not preserved in simple measures of β-diversity as among-site variability. There are, however, a number of ways that that can be accomplished, as we will describe.

10.1.2 Spatial location and environmental gradients

Location can also affect how diversity changes through space, either at geographic or at more local distances, acting through the patchiness just described or through monotonic gradients measured, detected, or inferred.

The heterogeneity among sites may be systematically related to the site positions on spatially explicit environmental gradients, which will be manifested in their characteristics as a function of physical location. The location of the sites being studied can be included in a multivariate analysis of species composition by using x (e.g. distance west) and y (e.g. distance north) coordinates as independent variables in the analysis (often x^2, y^2, xy, and so on may be included as well). This approach takes account of site location and can be used to partial out the variability in the data that can be attributable to location, but it does not remove the effects of spatial dependence on statistical tests (see below). Hence locational effects will often be confounded with the effects of environmental gradients, possibly not measured or considered. Under these circumstances, the diversity among sites will be more or less identical with β_T, the turnover diversity described in Section 10.2.2, but that depends on the controlling gradient(s) being overtly spatial and close to continuous or at least monotonic.

10.1.3 Spatial scale

The concept of scale includes a number of elements including *grain*, the size of the smallest discernible unit, and *extent*, the overall size of the area under consideration (see Chapter 1). Scale may be confounded with heterogeneity and location, but it includes also the sampling effect of total area, as in a collector's curve (e.g. a 'species–area curve', which plots the total number of species encountered as a function of the area searched), and nonlinear size effects.

At its most simplistic, scale as extent determines that more species are found, and perhaps that greater variability in the density of species already encountered is observed, as a larger and larger area is examined. This is not really truly a spatial effect if only area and not position is included in the analysis. A similar result might be predicted if a longer time period is substituted for a greater area. As subareas are aggregated into larger and larger combined samples, it is only area that is being considered, not spatial effects, unless the results are shown as dependent on which areas are aggregated. The same is true for any discovered nonlinear effects of area; they are not truly 'spatial' unless spatially explicit comparisons are included in the analysis. These effects are clearly both of interest to ecologists and ecological important; however, they are often not truly spatial, but areal in context and implication.

A number of studies have investigated the effects of scale as grain on measures of species diversity. The possible effects of changing grain are most easily understood by reference back to the effects of changing extent (Figure 10.1): if the organisms are randomly arranged point events in the plane, each with a given species label, a larger sampling unit has an increased chance of containing more species and a greater probability of containing at least one event of any given label, even if it is rare. As the unit grows, the frequency distribution of its collection of event labels approaches the overall distribution if they are randomly arranged, and evenness decreases toward the 'community' value. If the labels are not randomly arranged, but have local nonrandom variation in frequency, as if responding to environmental heterogeneity, larger sample units have nonlinear increases in observed richness as the units become large enough to include more than one environmental subarea within them. The observed unit diversity would continue to be considerably less than the community value (except for very large samples) because its collection would be

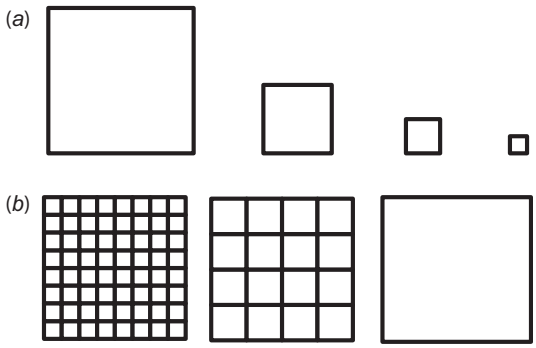


Figure 10.1 (*a*) Changing the size (extent and grain) of a sampling unit changes the probability that it contains any particular species, compared with (*b*) changing the grain of sampling. Both have strong effects on the measurement of diversity and the characteristics detected.

a biased sample of the overall community. Transferring this phenomenon to grain rather than extent is straightforward. Each contributing sample unit is affected similarly and the aggregate effects follow the same pattern.

One important example of this phenomenon is plant neighbour diversity, which is determined by the local composition of the neighbourhood (however defined) of the plants of a given species within a community. That neighbourhood composition, and thus its diversity, is not expected to be the same as for the more broadly defined community (Pacala 1997), whether because of particular ecological requirements and capabilities of the species in question or because the species modifies its own environment to the extent that it has a direct effect on the probabilities of finding other species there (Dale 1977). If there is a limit to the spatial range over whatever effects are in play, there is clearly a scale component to the phenomenon, but it is then confounded with propinquity or spatial dependence because the effect may be strongest close to the focal plant.

10.1.4 Propinquity and spatial dependence

This category includes the relative positions of samples and individual organisms, sometimes with a general understanding (which may not be true) that those that are close together have a tendency to be more similar.

Propinquity (closeness) will be interpreted here as including all relevant aspects of 'closeness' in spatial structure, not just the physical or geographic distances between the sites and the similarity or differences in their own characteristics (size, shape, and so on), but also their relative positions on environmental gradients, the connections or barriers between them, and the processes that make them functionally further apart or closer together (dispersal, migration routes, slopes, winds and currents, and so on). Propinquity then includes a quantification of spatial dependence, whether that spatial dependence arises from the biological variable under consideration, environmental variables on which it may be dependent, or a combination of the two acting together (inherent, induced, and double spatial dependence in the language of Chapter 8). Although the resulting spatial dependence is usually positive at short range, it can be negative, and in patchy situations, it can cycle between positive and negative with increasing distance. The often-cited understanding of decreasing similarity with increasing distance (e.g. by exponential decay) is only sometimes true, because patchiness can lead to a structure of similarity that initially decreases with distance, only to increase again (see Chapter 8 of this book). The decay of similarity with distance is considered to be a general law in geography ('Tobler's Law'; Tobler 1970), but it cannot be accepted as generally true of ecological systems. Clearly, of the four categories listed, the effect of propinquity or distance is the concept that includes most of the truly spatial aspects of second-order diversity.

As a simple experiment, whether in thought or on a computer, consider the following spatial model. A grid of cells is populated by a number of patches belonging to one of a finite number of different species (or colours) in such a way that (1) each patch is placed randomly, (2) each covers a set number of adjacent cells in a square or a circle and (3) each cell of the grid can be occupied by more than one species at the same time (see Figure 10.2). Each cell then has a 'composition' consisting of a list of the species it

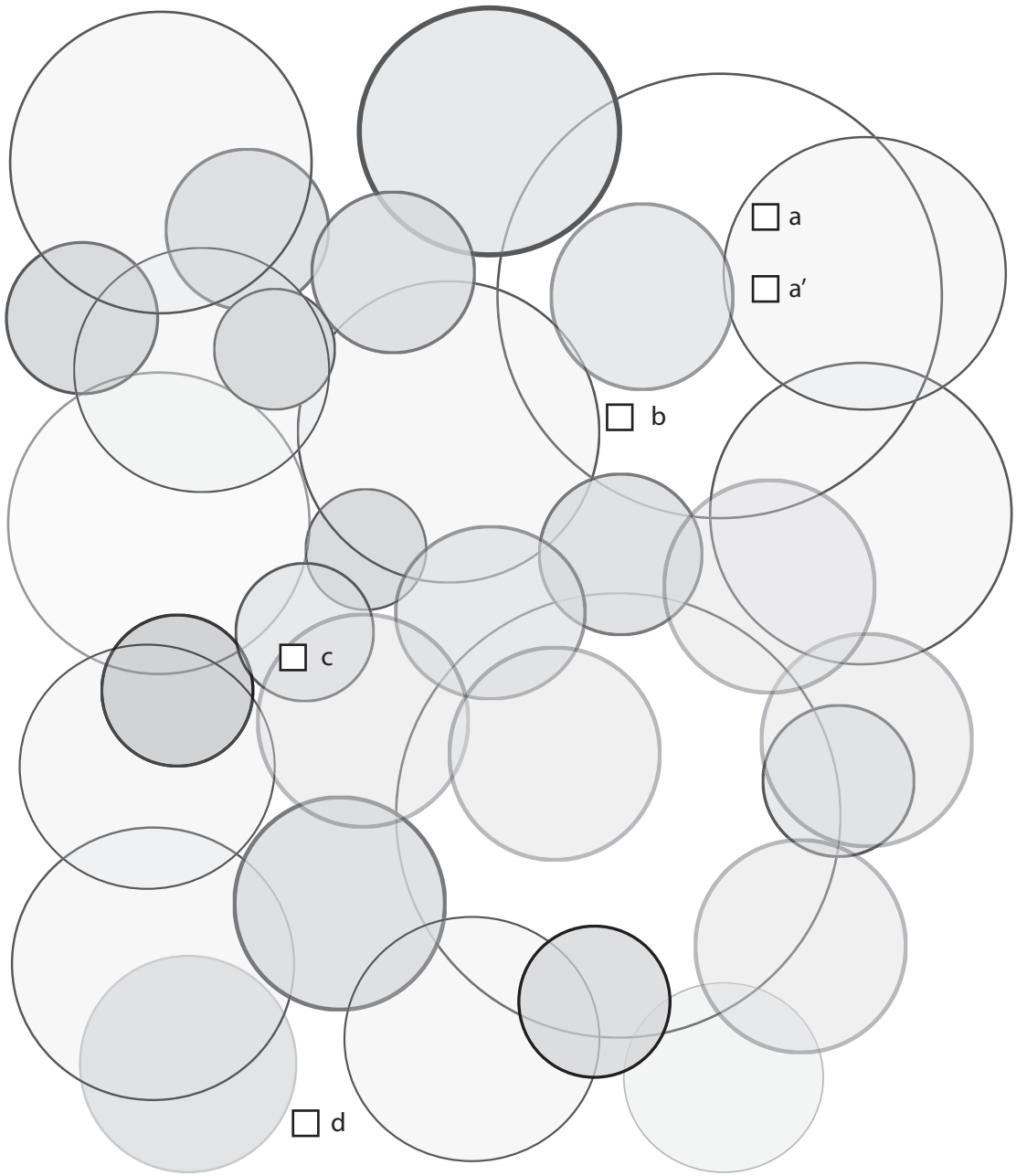


Figure 10.2 A community of possibly overlapping circular patches of different species results in greater autocorrelation in sample composition when the samples are close (e.g. locations labelled 'a' and 'a'' or 'a' and 'b', versus 'b' and 'd') even if the patches' positions and identities are random.

contains, including a number of species from zero to the total number available. Under those circumstances, there will be positive autocorrelation of species composition of cells that diminishes with distance, even though the patches have been randomly placed. For more sophisticated versions of this conceptual model, and for an excellent discussion, see Lantuéjoul's book (2002) on simulation models in geostatistics.

Many of the comments that can be made about spatial aspects of diversity measurement and analysis can also be made for the temporal dimension of such studies. It is not the main focus of this book, but we will make some comments on this topic to complement the discussion of spatial issues, particularly where the two interact. Before addressing the spatial issues related to diversity analysis, we will begin by describing the important concepts of ecological diversity in a non-spatial context.

10.2 First-order diversity

In ecological and related studies, diversity is a measure of unpredictability, beginning with the unpredictability of the species (or any category in some classification) to which a randomly chosen or 'randomly encountered individual' belongs. For example, given a forest of trees, the more species there are and the more equal their frequencies, the less easy it is to predict the species of a randomly encountered tree trunk, as is mostly the case in tropical rainforest (Condit *et al.* 2000). In this instance, diversity can be considered to be a measure of probability, but other units are possible for different versions of the diversity concept and index used. The fact that different measurement units apply for different measures of diversity (e.g. number of species or taxonomic distance are two more possibilities) can be used to clarify at least some of the confusion; for example, indices that have different units cannot be measuring the same thing. The basic definitions and measures of diversity begin with those suitable for a single 'collection', whether it is a sample or the contents of a single discrete census unit. There will be a difference between how the data are dealt with, depending on whether the information derives from a sample of a very large 'population' (in the statistical sense; perhaps in ecology meaning a well-defined community) or a complete census of all the organisms of interest in the study area. In a sample, the rarest of species may be missed so that the actual species richness is greater than the number of species in the sample and it is not known with certainty, whereas in a complete census, the true number is known. Techniques for calculation and interpretation have to be adjusted to take account of this difference (Scheiner *et al.* 2000; Chao 2004). The same comment applies equally to the abundances in a sample, compared to abundances known from a census. The analysis and interpretation of results may also be affected by whether the organisms or community being studied occurs in discrete 'natural sampling units' such as islands, ponds, or groves of trees, or whether we are studying samples or data from a more spatially continuous structure.

The concepts of diversity begin at the level of a single sampled site or a single fully enumerated area, but we can logically and usefully extend the concept to the next levels of organization. That next level of organization may be a subsequent stratum in a hierarchical organization of the samples based on spatial scale (e.g. sites to regions), non-spatial criteria (e.g. individual species to combinations of species), or classification system (e.g. a single criterion to a double or higher order of classification whether hierarchical or cross-classification). We can then extend any of these cases to include the spatial relationships between individuals within the samples or among the samples themselves in order to provide an analysis of spatial diversity, as we will describe in subsequent sections below. The most common organization of diversity into levels is based on spatial considerations of area, and defines three levels: α-diversity for within sites, β-diversity for between or among sites, and γ-diversity for an entire region (Whittaker 1977). Figure 10.3 illustrates this classification, and we will begin by following that order of presentation.

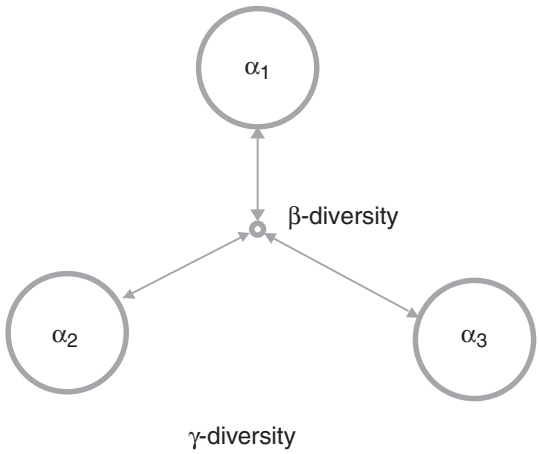


Figure 10.3 A single collection gives α-diversity and the entire area of study gives γ-diversity; the second intermediate level is β-diversity, the diversity among or between primary sites or samples.

10.2.1 α-diversity

At the lowest level of any hierarchy of biological diversity is some measure of the diversity in a single collection using a single classification of the organisms present. Usually, the single collection is taken to be a site, but it is possible to have several samples per site. The term 'α-diversity' is applied when evaluating the contents of a single collection, sample, or sample unit (Crist *et al.* 2003; Anderson *et al.* 2006). The diversity at a site often will be based on a number of samples, whether distributed through space, as quadrats for sampling vegetation, or distributed through time, as in trapping sessions for flying insects, or both. Probably the most important feature of α-diversity is that it changes with the extent and intensity of sampling, whether in space or in time, producing (for space) a species–area curve (diversity as a function of area sampled); this is one basic version of a spatial effect in diversity studies. Therefore, the *α*-diversity measured is affected by spatial scale, both as grain of sampling and as extent (see Figure 10.1).

Turning to the measurement of diversity, there are several questions that arise in developing or choosing a measure of diversity at this level. Is this a complete census of the organisms, or truly a sample of those that are present? If it is a sample, what is the relationship between the area of the site about which inference is to be made and the total area covered by the samples? Are there measures of abundance for the classes that are being used or just presence : absence data? How certain is the identification of the organisms and the taxonomy of the classification used?

In general, the assumptions for evaluating diversity at a single site include at least (1) that all identified taxa are treated as equivalent, (2) that the measure of abundance is appropriate for the kinds of organisms under study, and (3) that where 'individuals' are used as the basis for calculation, all individuals are treated as equivalent (Peet 1974). Many measures of diversity combine both the number of taxa, known as 'richness' and the equality of their representation in the data, known as 'evenness'. The many measures available combine the two with various degrees of relative influence on the final value of the index and the relative influence of rare versus common taxa on the outcome (Magurran 2004). The two most common measures that combine richness and evenness for abundance data are Simpson's index, D_S, based on probability, and the Shannon–Weaver index, H', based on information theory, both of which use the proportion of the total abundance, however measured, that belongs to the ith category of the s in the classification, p_i:

$$D_S = 1 - \sum_{i=1}^{s} p_i^2 \text{ and} \tag{10.1}$$

$$H' = -\sum_{i=1}^{s} p_i \log_e p_i. \tag{10.2}$$

Simpson's index, D_S, is usually formulated as the probability that two randomly chosen individuals (however defined) belong to different species. It can also be interpreted as the 'per individual' variance in the data set when represented as an s-dimensional space with the n_i individuals (or equivalent) of species i one unit from the origin

on the ith axis (Lande 1996). There are several very positive features of the information theoretic index as well (Pielou 1979), despite ongoing criticism of the difficulty of interpreting its value (Magurran 2004, p. 101), especially the ability of the measure to be partitioned by source when more than one classification is applied (see Section 10.4) and its relationship with the log-likelihood ratio statistic for contingency table analysis.

Given the great variety of measures of diversity that have been proposed, we will not even begin to include them all, but we will mention Hill's (1973) scheme to unify at least some of the measures, with what are now referred to as Hill's diversity numbers. The insight was to investigate a general form of a diversity index, which is

$$N_x = \left[\sum_{i=1}^{s} p_i^x\right]^{\frac{1}{1-x}}. \qquad (10.3)$$

When $x = 0$, we get $N_0 = s$; for $x = 1$, $N_1 = e^{H'}$; and for $x = 2$, $N_2 = (1 - D_S)^{-1}$. N_1 is sometimes known as the 'effective number' of species, because it is equivalent to the number of species that, if all species were equally represented, would give the same value of H'. Each of these several measures has its own advantages and disadvantages, as well as proponents and detractors. We will not attempt to review the long list of measures here, but will refer to Hill's original explication, and to more recent summaries such as Magurran (2004) or Jost (2007).

10.2.1.1 Spatial structure

There are a number of ways in which a study at a single site may give rise to the need for an analysis of the spatial structure of diversity. The methods cannot be universally used because they require spatially explicit sampling, which may not always be available or possible, but are nevertheless relatively common. Examples of data collection designs that permit certain kinds of single site spatial analysis include the use of several traps within a site, say pitfall traps for ground-dwelling arthropods or light traps for flying insects; spaced or contiguous arrays of quadrats for sampling bryophytes, forbs, grasses, and so on; and especially the direct mapping of the positions of spatially discrete organisms such as sessile molluscs on a rocky shore or tree stems in a forest.

In Chapter 1, we introduced the distinction between global measures that apply over the whole study area, and local measures that apply over a much smaller area and are associated with a particular location. In the same way, when considering species diversity, we could divide the study area, for which we have calculated some diversity measure, into 100 subareas and recalculate the same diversity measure for each subarea. In this case, we could then maintain the importance of the spatial configuration, by doing more than partitioning within and between subarea diversity, by actually creating a map of the subarea indices (Figure 10.4*a*). We might argue that the choice of subarea size and number is arbitrary and we would certainly expect the results to change with the scale of the sub-unit chosen. In many cases, there may seem to be no spatial scale that is 'natural' in the sense of being related to the sizes and arrangements of the organisms themselves. However, in a forest or a meadow of forbs, it could be argued that by using the stem as an 'individual', natural subareas could be created using (say) the first-order neighbours of each stem in a Voronoi polygon scheme (Chapter 3 of this book). Each subunit, and the measure of diversity calculated for it, could then be associated with the spatial location of the focal stem (Figure 10.4*b*). In addition, maps of the diversity scores of all stems could be used to examine the spatial variability of diversity throughout the study area.

A second way of using the stem-by-stem diversity scores would be to summarize them by species. Better yet, the diversity of neighbours of stems of any given species could be evaluated using the frequency distribution of all species in neighbourhoods of stems of any given species. If the occurrence of plants of different species were independent, the neighbour frequency distributions would all be estimates of the common overall frequency distribution,

(*a*) Quadrat diversity of a grid

0.54	0.71	0.80	0.72
0.64	0.67	0.77	0.74
0.76	0.78	0.76	0.72
0.79	0.76	0.71	0.70

Whole area 0.78
Average of subareas 0.72

(*b*)

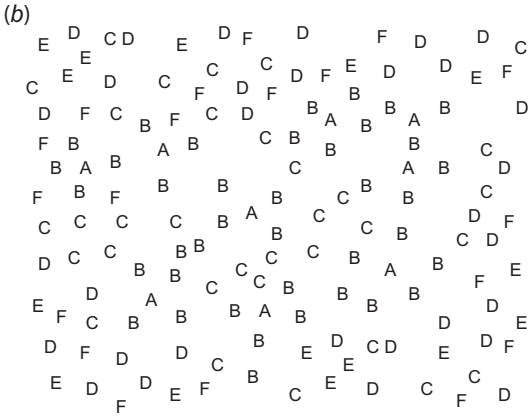


Figure 10.4 (*a*) The diversity of subareas may be affected by the details of the subdivision of the study area, and the average is unlikely to be the same as the diversity overall. (*b*) The diversity of neighbours experienced by an individual can be very different from the overall diversity of the community or sample. For example, individuals of species A in the figure experience a nonrandom sample of the community, with species B as a common neighbour and species E rare.

but in real plant systems, that is not expected to be true. In fact, the realistic ecological expectation is that the species list of neighbours of plants of species A is going to be substantially different from the list for the whole study area. Pacala's (1997) 'spatial segregation hypothesis' suggests that this difference, which shows up in the non-independent frequencies of neighbours, 'enhances ecological stability (resilience) and biodiversity'. Different neighbour lists and different neighbour diversities for every species, combined with nonrandom species occurrence, can amplify the heterogeneity observed in a plant community.

The concept that the neighbours of the plants of any given species are a nonrandom selection of those in the whole community is also familiar from the approach to studying plant communities by looking at the association, positive and negative, between species in the community. Positive association refers to the tendency of the plants of two (sometime more) species to be found together more often than expected from independence, and negative association refers to the tendency to be found together less often. Both positive and negative association can be caused by direct interactions between the plants (facilitation or competition) or by similarities or differences in their ecological requirements and capabilities (Dale 1977). Species association can be determined from counts in quadrats (their size having an effect on the outcome), or by counts of neighbours, however determined.

Neighbours can be determined by a hierarchy of networks based on distance and topology as described in Chapter 3 of this book. Even within a single network, there is a hierarchy of neighbours: first-order, second-order, and so on. Neighbours can also be determined by a series of threshold distances, again giving rise to a non-decreasing list of neighbours for any plant under consideration. For any definition of neighbours, almost any index of species diversity (or richness or evenness) can be calculated, averaged, mapped, and so on. For example, Shimatani (2001) advocated an index of diversity based on the probability that 'randomly chosen pairs' of plants belong to different species (essentially Simpson's index; Section 10.2.1) for multivariate point data, to study how the diversity of tree stems changes with distance. Shimatani's method is essentially the same as the multivariate Ripley's K, as described in Chapter 4 of this book, for all interspecific pairs of events, designated as $K_{X,\sim X}$,

and the transformation that allows a comparison of the observed and the expected as a function of distance t. In the notation of this book, it is

$$\hat{K} = \sum_{i=1}^{N} \sum_{j \neq i}^{N} [w_{ij} I_t(i,j) | m(i) \neq m(j)] / N^2. \tag{10.4}$$

This is the corrected count of the number of pairs of events, within distance t of each other, that belong to different species. In Shimatani's version, $\alpha(r)$ is the probability that two randomly chosen tree stems, separated by a distance no more than r, belong to different species; this is Simpson's index with a distance condition. The two are obviously very closely related, with the main difference being that the modified Ripley's K can take both positive and negative values with magnitude greater than 1.0, whereas $\alpha(r)$ can take only values between 0 and 1.

An alternative approach, which can be used when the organisms are not easily or justifiably reduced to dimensionless points for which neighbours in a series of neighbourhoods can be determined, is to use a moving window of a set size and shape for which an index of diversity is calculated over a range of possible positions. There is no reason not to use this technique even when the organisms can be treated as dimensionless events with only the characteristics of location and species. This approach is very much in the spirit of using local statistics to evaluate spatial variation in characteristics that are otherwise evaluated as a single value for the entire study area, just as a scan statistic examines spatial data for local 'hot spots' of high values. The approach is also in line with the 'template' concept, which we have emphasized as a conceptual tool for developing and understanding spatial statistics. Although not originally intended to illustrate this point, the example of the Lansing Woods data, divided into subplots (Figure 10.4*a*), shows how the calculation of a diversity index for subareas of a study can help identify 'hot' and 'cold' regions of tree diversity.

10.2.2 β-diversity

As the term 'α-diversity' is used for the characteristic of a single collection, the second level of diversity analysis is usually designated 'β-diversity' (Whittaker 1977), referring to the diversity among sites or among samples within a region, each with a measurable α-diversity and each contributing to the total regional diversity, usually called 'γ-diversity'. Despite this origin, the concept and measure of β-diversity need not rely on the other two hierarchical levels of diversity, but it can be defined and estimated directly from the total variance in a site-by-species community data table of frequencies or equivalent (Legendre *et al.* 2005). However approached, the topic of β-diversity can be quite complicated (Vellend 2001; Koleff *et al.* 2003; Crist *et al.* 2003; Jost 2006; Harrison *et al.* 2006; Anderson *et al.* 2011), in part because the term is used to refer to several distinct concepts, which may overlap in a number of ways. For example, there is a conceptual difference between what may be found at a series of sites that occur along a clear and explicit environmental gradient, and what may be found where no such gradient is effective or evident.

10.2.2.1 β-diversity with gradient not assumed

The first version of β-diversity is based on the partitioning of the total diversity, using M to represent any measure of diversity and subscript T for total, for some classification of the objects under study, classification C, which can be interpreted also as the set of s categories being used, measured in a number of sites or habitats of a given study area or region into those parts attributable to diversity *between* sites (designated B) and diversity *within* sites (designated W):

$$M_T(C) = M_B(C) + \overline{M}_W(C), \tag{10.5}$$

where $\overline{M}_W(C)$ is the (possibly weighted) average of within-site diversities:

$$\overline{M}_W(C) = \sum_{j=1}^{m} q_j M_j(C), \tag{10.6}$$

with the q_j being weights that add to 1.0 (often they are equal).

In ecological studies, a common division of species diversity in a spatial context uses the designation of α for site diversity, β for local or differences in site

diversity, and γ for regional or total diversity. Using that notation and the bar again indicating the average, the partition becomes

$$M_\gamma = M_\beta + \sum_{j=1}^{m} q_j M_{\alpha j} = M_\beta + \overline{M_\alpha} \text{ or} \tag{10.7}$$

$$M_\beta = M_\gamma - \overline{M_\alpha}. \tag{10.8a}$$

Depending on the technicalities of the measure of diversity used (replacing M with M', say); the relationship can also end up being

$$M'_\beta = M'_\gamma \div \overline{M'_\alpha}. \tag{10.8b}$$

In the additive version (Eq. (10.8a)), all three measures have the same units, such as 'species equivalents' perhaps, whereas in the last multiplicative relationship (Eq. (10.8b)), α-diversity and γ-diversity are measured in the same units, but the measure of β-diversity is different, having no units because it is a ratio.

Although there is a spatial context to this scheme, having areas and subareas, there is no spatially explicit component to the concept, or to the measures derived from it, because the spatial structure is not included in any way: the spatial relationships of the subareas, their relative sizes, distances between, and relative or absolute locations are not included in the measure. Including space is possible, however, for example by comparing the set of pairwise differences in point diversities with the set of pairwise geographic distances between the subareas (Legendre *et al.* 2005; Tuomisto & Ruokolainen 2006; and related correspondence).

In some cases, the three-level system of α, β, and γ seems insufficient, and authors subdivide the level of β-diversity. For example, a study of the diversity of tree canopy beetles by Crist *et al.* (2003; repeated in Lande *et al.* 2003, table 7.4) used four levels: β_1, among trees within stands; β_2, among stands within sites; β_3, among sites within regions; and β_4, among regions (Figure 10.5). The advice of Rosenzweig (1995, p. 33) is not to rely on levels such as these, but they may be useful, particularly in the context of partitioning diversity (Gering *et al.* 2003; Legendre *et al.* 2005; Ricotta 2005). This scheme is hierarchical, but it need not be spatially explicit.

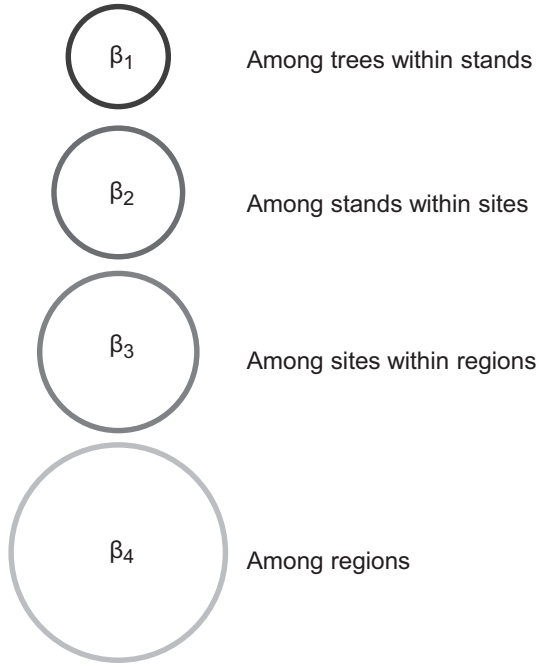


Figure 10.5 A possible hierarchy of levels of β-diversity, denoted by subscripts, based on spatial or organizational scale, such as trees within stands, stands within sites, and so on.

A next step from any level of diversity evaluation is to include the spatial structure of the system being studied in the evaluation. As a simple version, each sampled site has its position recorded, say in *x*–*y* coordinates, and perhaps other spatially relevant characteristics such as area, elevation, moisture regime, and so on. The easy approach is to calculate a measure of first-order diversity (even if merely as species richness, the number of species observed) for each of several sites, and then to compare differences in that measure between pairs of sites with geographic distances between them, using a Mantel test. A Mantel test compares the matrix of site-to-site differences in diversity or composition (for example, richness is often used) with the matrix of site-to-site physical distances and produces a single measure of the similarity of the two matrices which can be tested for significance by randomization procedures (Legendre & Fortin 2010).

Diversity at sites on a gradient

Sites	1	2	3	4	Density
Species present					
	A	B	C	D	1000
	B	C	D	E	500
	C	D	E	F	100
	D	E	F	G	20

With or without the densities of organisms of each species present at the sites, all sites have the same diversity index, although having different compositions.

Figure 10.6 Diversity at sites 1 to 4 on a gradient showing the species present at each site (four of the seven species, A to G, at each) and their densities. Any measure of diversity will give identical values for all four sites, when considered separately, although the composition varies greatly.

The problem with this suggested approach is that it does not recognize that α-diversity, including simple species richness, is a synthetic variable and so two sites may have similar values even if the species lists are very different. Figure 10.6 provides a simple artificial example in which richness and diversity are both identical over four sites on a gradient, despite the obvious fact that species composition is changed markedly from one site to the next. In some applications, similar diversity (as such) may be the focus of the study (particularly if diversity is remarkably high or remarkably low), but often the interpretation will be linked to assumed similarities in community composition which may be true in some cases, but quite misleading in others (Cayuela *et al.* 2006).

The second problem with using the Mantel test in this way is more general as described elsewhere (see Fortin & Payette 2002; Dietz 1983; Legendre & Legendre 1998; Legendre & Fortin 2010). Briefly, the problem is that the Mantel test works best when there is a linear relationship between the dissimilarity for the variable of interest and physical distance. Therefore, if the dissimilarity measure increases with distance, producing negative autocorrelation over a middle range of distances, and then decreases again, as we find with patchy data, the correlation between the measure and distance will be approximately zero, overall, and the Mantel approach will not find it significant. Therefore, the Mantel approach may be less useful under these circumstances than would be hoped based on the assumption of increasing dissimilarity with increasing distance. If the relationship is monotonic then a Spearman's rank Mantel test can be used (Dietz 1983; Legendre & Legendre 2012).

A second approach is to use species composition itself in a direct way, rather than using the summary of a diversity index, and to calculate differences in species compositions between pairs of sites using any of a number of dissimilarity coefficients (based on presence : absence data or on abundances), and then compare those with geographic distances using the same Mantel method described above. This leads us to the discussion of species composition complementarity in Section 10.3.

Other techniques for studying spatial structure of diversity will be described below, to include the actual locations of the samples and the identities and characteristics of the samples that can be considered to be neighbours. In a spatially explicit approach, McKnight *et al.* (2007) mapped β-diversity calculated from a moving window to estimate the decay of compositional similarity with distance. This was a study at geographic scale, using a grid of 100 × 100 km cells, but the authors were able to compare the results for three taxonomic groups: birds, amphibians and mammals. The areas where there were high levels of differentiation matched for the three groups, but the areas of low turnover and thus greater homogeneity did not match.

10.2.2.2 β-diversity with spatially explicit gradient

The second approach to β-diversity depends, at least initially, on the sites being arranged along an explicit environmental gradient, with some species that are present at the beginning of the gradient dropping out from the species list (the number of species losses is l) and others that are absent at the beginning being

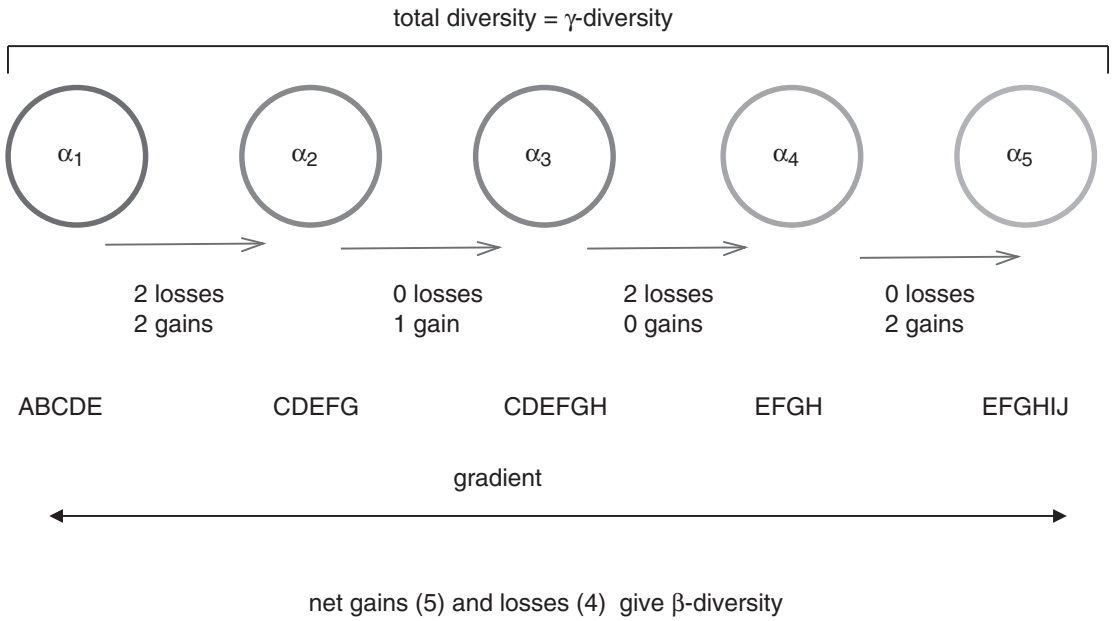


Figure 10.7 The concept of β-diversity based on species turnover along a gradient. Here are five sites with species compositions given by lists (A to J), showing losses and gains of species between adjacent sites. Turnover β-diversity is the total net losses and net gains, each compared to the average richness (5.2) for the sites: $\beta_\tau = (4 + 5)\ /(2 \times 5.2) = 0.87$.

added (the number of species gains is *g*), with the potential of being lost farther along the gradient (as illustrated in Figure 10.7). This phenomenon of gain and loss of species at sites along a gradient is often referred to as 'turnover', but the term is somewhat ambiguous because it is conceivable that a species with a bimodal distribution could appear and disappear from the species list more than once along the length of the gradient or that a species might make a brief appearance in the record, appearing and disappearing between the first and the last sample in the series. The associated measures are usually an accounting of net losses and net gains from beginning to end. This version of β-diversity, call it β_τ, with τ for turnover, is essentially spatially explicit for obvious reasons in a way that other versions of the concept are not. What is not addressed is whether the unpredictability that is measured by a diversity index in this case is a function of position along the gradient, and along the transect used to sample it, or a function of the other species found at the sites. This β_τ, turnover diversity, is a function of numbers of species lost and gained along the length of the transect, either in cumulative counting where a species both gained and lost adds to both totals or in net accounting where such a species adds to neither. A closely related concept is that of the length of gradient required to cause a turnover of half the average number of species at any site, and this is sometimes formulated as a measure of compositional change, sometimes called a *Gleason* (Wilson & Mohler 1983). Other formulations of β_τ are possible, based on calculations more like those used to compare among-site diversity to within-site diversity. With a spatially explicit gradient, this investigation of β diversity is truly spatial analysis in a single dimension.

In comparing the no-gradient version with the explicit-gradient version, Vellend (2001) showed that if species turnover is limited to losses and gains between the first plot and the last, and if the numbers of species in the terminal plots are close to the average richness, then the two versions of β-diversity are essentially measuring the same thing (Wilson & Shmida 1984).

This equivalence is dependent on the spatial arrangement of the plots which must reflect the change of species along a gradient. Therefore, despite the equivalence under special conditions, general measures of β-diversity are not appropriate for measuring species turnover as such, and when the focus is on changes of composition along a gradient, measures of compositional similarity as a function of distance would be more explicit indicators of that kind of change. This is because one consequence of the spatial structure is that the similarity between plots decreases with distance between them. This is a safe assumption for samples on an environmental gradient, but less easily defended as a general rule where the patchiness of natural systems may work against the assumption (Soininen *et al.* 2007; Nekola & White 1999). On the other hand, if the gradient is long enough, the ends of the gradient may appear similar because both ends lack the species that are common in the middle portions of the gradient; this is something like the horseshoe effect in ordinations which require detrending (Legendre & Legendre 2012). Another consideration is that other features of community composition such as nestedness, where rare species occur only at the richest sites, may be confounded with turnover in general measures of β-diversity and may have to be partitioned out to provide clarity of the contributing effects (Baselga 2010).

If it is not known that the sites or samples are arranged on a clear or simple gradient, it still makes sense to consider the spatial structure of diversity as 'spatial variation in β-diversity' (Koleff *et al.* 2003). In that case, because at least two sites are required to calculate β-diversity whatever the spatial location, it is advantageous to begin the assessment of between-sample diversity with an evaluation of pairs of samples. Then, measures of diversity and measures of (dis)similarity for presence : absence data converge. These can be based on the entries in a 2×2 contingency table for each pair of *samples*, based on numbers of species that are present in both samples, *a*, the number of species present in the first but not the second, *b*, and so on. For quantitative data, the equivalent approach is to use the correlation between species abundances at the two sites as a measure of their similarity, just as correlation between species abundances at different sites can be used to evaluate the relationship between any pair of species (Ludwig & Reynolds 1988).

Much greater clarity can be achieved when the spatial structure is arrayed along a single spatially explicit gradient. It seems easy then to relate changes in composition and diversity to a unidirectional change in controlling environmental factors, such as physical conditions of temperature, moisture, and so on. It may not be so easy, however, because 'natural gradients are almost always very complex, with many different physical factors changing along the gradient, some increasing while others decrease. Likewise, the diversity of different components of the natural communities along a gradient may change in very different ways' (conclusion to chapter 2 of Huston 1994).

Whatever the difficulties, the existence of spatially expressed gradients gives rise to a particular kind of propinquity in which, for the most part, physical closeness brings a similarity of conditions encountered or endured, as well as the greatest opportunity for interactions between the organisms to occur, without the intervention of great differences in environmental conditions. (The latter comment is scale-dependent both in the sense of scale as grain, and in the sense of scale as extent.) In this particular version of propinquity, 'next to' combines spatial and environmental proximity, and the connection is made easier by the gradient's (conventional or assumed) single dimension of functional importance. In this way, at least, temporal series resemble these spatially explicit gradients.

10.2.2.3 β-diversity with more than one gradient

The possibilities and difficulties described for the analysis of β-diversity on a single explicit gradient are amplified when there is more than one such gradient to be considered. This topic is one of much discussion and active methodological research at the time of writing, and we cannot offer a finalized summary of their outcome. The question is whether the directionally explicit methods related to turnover make sense within a more complex spatial structure underlying the data, such as more than one gradient. With more than one gradient, as for a single gradient, physical closeness will create a certain similarity of

conditions, which should be reflected at least partially in species composition, and methods of analysis will have to account for that localized version of similarity or of change in any spatial direction. The treatment of the data should still be directional because there are gradients, but there is more than a single direction to be considered. The approach based on partitioning looks like a convincing advance (Legendre *et al.* 2005; Legendre 2008), particularly when the contributions of individual sites to β-diversity can be mapped as a function of location and thus related to the environmental gradients (see Legendre & De Cáceres 2013). The reader is also referred to Tuomisto (2010a, b, parts 1 and 2), Chase *et al.* (2011), and Chao *et al.* (2012) for further discussion. We predict continued interest and further developments in this area of research in the near future, and perhaps, as the title of Chao *et al.* (2012) optimistically predicts, some resolution of the current disagreements.

10.2.2.4 β-diversity for pairs: two sites or two samples

For a number of reasons, we may want to compare the diversity at pairs of sites or in pairs of samples, and the β-diversity that is that comparison will be simply a particular instance of the measures given above, with or without a gradient. We may be especially interested in comparing the diversity at a pair of sites by using a graph theory approach and spatial graphs (Chapter 3) to study the spatial structure of diversity.

For presence : absence data, the pair measure is essentially a measure of 'turnover' (β_τ) between the sites, the number of species lost and the number gained. For only two sites, with s_i species at one site and s_j at the other, and $s_{i\&j}$ at both, the turnover count is:

$$\beta_\tau = s_i + s_j - 2s_{i\&j}, \tag{10.9}$$

with the proportional change being

$$\beta_p = (s_i + s_j - 2s_{i\&j})/(s_i + s_j - s_{i\&j}). \tag{10.10}$$

In more familiar notation, this is the Jaccard distance of $(b + c)/(a + b + c)$, where a is the number of species common to both sites, and b and c are the numbers of species found at only one of the sites. Another frequently used distance measure for this context is the Sørensen index, $(b + c)/(2a + b + c)$.

The complement of distance measure is a similarity measure: $S_p = s_{i\&j}/(s_i + s_j - s_{i\&j})$, being the proportion of species that are common to both sites. This is the Jaccard coefficient of similarity: $a\ /(a + b + c)$.

For abundance data, the correlation coefficient of the abundances of species that are present at one or both sites is a good candidate measure of similarity, with its complement being a measure of diversity, but there are lots of possibilities for measures of differences in multivariate composition (see Legendre & Legendre 2012 for a table of these). For example for our two sites having relative abundances of species k of $p_{i,k}$ species at one site, $p_{j,k}$ at the other, and $p_{i\&j,k}$ at both, a simple diversity measure would be based on the Simpson index as:

$$\beta_d = \sum_{k=1}^{s_{i\&j}} \left[(p_{i,k})^2/2 + (p_{j,k})^2/2 - (p_{i\&j,k})^2 \right]. \tag{10.11}$$

A similar measure can be based on information theory:

$$\beta_d' = \sum_{k=1}^{s_{i\&j}} \left[p_{i,k}\ln(p_{i,k})/2 + p_{j,k}\ln(p_{j,k})/2 - p_{i\&j,k}\ln(p_{i\&j,k}) \right]. \tag{10.12}$$

For any pair of sites, Baselga (2010) proposed that we can partition the β-diversity measured by the Sørensen index, mentioned above, into the components attributable to turnover and to nestedness. Here nestedness refers to the tendency of species-poor sites to have only the most common species and of rare species to occur only at the richest sites. The proposed partition is:

$$\beta_{SOR} = (b + c)/(2a + b + c) = \beta_{TUR} + \beta_{NES}, \text{ with}$$
$$\beta_{TUR} = \min(b, c)/[a + \min(b, c)], \tag{10.13}$$
$$\beta_{NES} = \{[\max(b, c) - \min(b, c)] \div [2a + \min(b, c) + \max(b, c)]\} \times \{a/[a + \min(b, c)]\}.$$

Re-write this as:

$$\beta_{NES} = [|b - c| \div (2a + b + c)] \times \{a/[a + \min(b, c)]\}. \tag{10.14}$$

We will illustrate the usefulness of this partition in an example in Section 10.2.4 of this chapter. As previously stated, the major application of the site-pair β-diversity evaluation is probably for the creation of weights for the edges of spatial graphs depicting diversity characteristics in a spatial context, or to look at very local patterns of diversity. On the other hand, Legendre & De Cáceres (2013) showed how the matrix of pairwise dissimilarity coefficients can be used as the basis for the overall evaluation of β-diversity in the entire data set.

10.2.3 γ-diversity

This level of diversity, γ-diversity, is the highest we will consider, covering the largest spatial extent, being that of the entire region of study, but we will not make too many detailed comments. Clearly γ–diversity is affected both by spatial extent, a frequent focus of γ-diversity studies, and by spatial grain, especially when grain affects the ability to detect or to measure the abundance of rare species. It can have large effects on some estimates of β-diversity, because it represents the measure of total diversity from which β-diversity measures are extracted by partitioning. The estimate of γ-diversity sets limits on the interaction of the other two measures, α-diversity and β-diversity. The other interaction between γ-diversity and spatial structure and spatial analysis is that in the 'ecological play' spatial partitioning can enhance the coexistence of competing species or provide partial refuge for prey, for example, thus increasing total diversity. At evolutionary spatial and temporal scales, spatial partitioning also may play an important part in evolutionary diversification and species coexistence, also leading to higher amounts of overall diversity (Nosil & Rundle 2009; Amarasekara 2009).

Within the general field of ecology, there has been developing and maturing in recent years the subdiscipline called macroecology, which looks at the relationships between organisms and the environment at large spatial scales, focusing on abundance, distribution, and diversity (Brown 1995; Gaston & Blackburn 2000; Marquet 2009). It has grown out of, but is not identical to, some of the topics originally included in what was termed biogeography. Although there is a clear link between some aspects of what is now included in macroecology and some topics in spatial analysis, such as species–area relationships or spatial turnover of species, there are a large number of topics within macroecology that are not comparable, such as the relationships between body-size and extinction or between species richness and energy (for a partial list of topics see Gaston & Blackburn (2000), their table 1.1). For that reason, we will not place as much emphasis on macroecology as we may in future years, as the relationship between it and spatial analysis becomes stronger (see Marquet 2009). Perhaps the closest relationship between macroecology and spatial analysis is in the consideration of the factors that determine γ-diversity and the possible roles of physical structure (e.g. insularity and environmental gradients), spatial extent (species–area relationships) and spatial autocorrelation in γ-diversity studies. (For the last topic see Lennon 2000; Diniz-Filho *et al.* 2003; Dormann 2006; and many others.)

10.2.4 Why space in first-order diversity analysis?

To conclude this section on diversity, it may be useful to include a couple of artificial examples that illustrate the importance of spatial structure in understanding diversity analysis.

Example 1

In this example, 600 individuals are sampled in 5 sites (sites 1 to 5) as shown in Table 10.1. The number of individuals per site ranges from 105 to 135 and the proportion of individuals belonging to species A (260/600) ranges from 35/105 to 75/135. There is a trend in the dominance of species A from site 1 through to site 5. When the locations are ignored, the composition of the sites is consistent with the null hypothesis of random subsets. However, when the locations of the sites and their neighbour relations are taken into account (they are a chain of islands), the trends are obvious and the hypothesis should actually be rejected. Ignoring space leads to the wrong conclusion.

Table 10.1 Example 1

Sites:	1	2	3	4	5	Total
Species A	35	45	50	55	75	260
B	20	25	20	30	20	115
C	20	15	15	10	15	75
D	15	15	20	15	10	75
E	15	20	15	10	15	75
Total	105	120	120	120	135	600

The details are that the initial non-spatial test is a standard goodness-of-fit test ($G = 26.23$, n.s. at $\alpha = 0.05$). While there seems to be trend in the data, most obviously in the dominance of species A, it would be incorrect to test for this trend using, for example, a Cochran–Armitage test based on the data alone. The sites, however, represent a chain of islands, 1 to 5, with species A being the most dispersal-limited, and so there is a priori justification for a Cochran–Armitage test based on the spatial structure of the data. On that basis, the Cochran–Armitage test is justified and provides a significant result, indicating a trend ($T = 5.24$, $p < 0.0001$). This example is similar to the original from Cochran (1954) described again in Agresti (1990, p. 100), in which a general goodness-of-fit test is not significant, but a test for a trend is significant. In the spatial context we consider here, the only wrinkle is that if the sites are not islands, but samples that are close together in a continuum, the test may require correction for spatial autocorrelation in the data, based on the calculation of an 'effective sample size' (see Dale & Fortin 2009).

Example 2

In this example, illustrated in Figure 10.8 and Tables 10.2 and 10.3, the 12 samples are taken on three branches of a river, designated as $x = 1, 2, 3$, with four samples on each, with $y = 1$ being near where the branches join and $y = 2$, 3, and 4 being further upstream. Species A and B occur at the downstream sites, and species J is found only at the head of the tributaries. Species C and D, E and F, and G and H are found mainly, but not exclusively, in the three different branches $x = 1$, 2 and 3. Without knowing the spatial locations of the sample, the pattern of presences and absences that contribute to the sample diversities is very difficult to interpret. Using the multisite measures described in Baselga (2010) and explained in a preceding section of this chapter (Section 10.2.2), $\beta_{SOR} = 0.75$, $\beta_{TUR} = 0.5063$, and $\beta_{NES} = 0.2437$, suggesting that the structure has twice as much turnover (indicated by β_{TUR}) as it has nestedness (β_{NES}). The measures of diversity used here are equally aspatial, but they can clearly have a spatial interpretation in a spatial context such as this one.

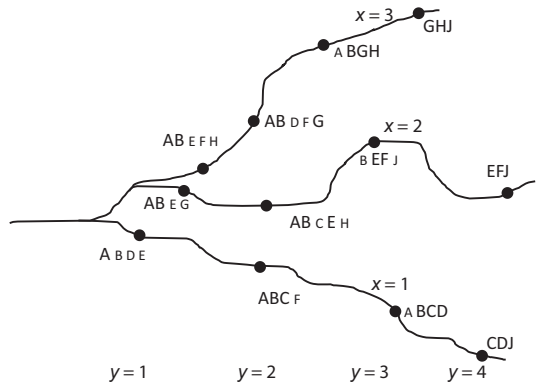


Figure 10.8 The importance of spatial structure in diversity studies: three branches of a river with community compositions for various locations: letters for species, with the larger font representing the most abundant at each site. The positions in the drainage system help interpret the patterns of diversity.

Neither example is particularly sophisticated, but they both provide good mimics of the kinds of situations encountered in diversity analysis of field data when the spatial structure is not, at first, explicitly included in the analysis.

Table 10.2 Aspatial summary

B	A	E	F	C	D	G	H	J	total	(x, y) location
■	■	+	+				+		5	(3,1)
■	■		+		+	■			5	(3,2)
■	■	■		+			+		5	(2,2)
+	■	+			+				4	(1,1)
■	■		+	■					4	(1,2)
■	+			■	■				4	(1,3)
■	■	+				+			4	(2,1)
■	+					■	■		4	(3,3)
+		■	■					+	4	(2,3)
				■	■			■	3	(1,4)
		■	■					■	3	(2,4)
						■	■	■	3	(3,4)
9	8	6	5	4	4	4	4	4		← Totals

The square symbol indicates high abundance, the plus sign indicates presence with low abundance, and a blank indicates absence.

Table 10.3 Spatial summary

$x = 1$

sp:	A	B	C	D	E	F	G	H	J
$y = 1$	■	+		+	+				
2	■	■	■			+			
3	+	■	■	■					
4			■	■					■

$x = 2$

sp:	A	B	C	D	E	F	G	H	J
$y = 1$	■	■			+		+		
2	■	■	+		■			+	
3		+			■	■			+
4					■	■			■

$x = 3$

sp:	A	B	C	D	E	F	G	H	J
$y = 1$	■	■			+	+		+	
2	■	■		+		+	■		
3	+	■					■	■	
4							■	■	■

The square symbol indicates high abundance, the plus sign indicates presence with low abundance, and a blank indicates absence.

10.3 Species combinations and composition: agreement and complementarity

We have described the concept of diversity informally as a measure of some sort of unpredictability of composition, but the measures of biological diversity that are based only on species disorder do not summarize adequately the structural complexity of ecological communities (Ricotta & Anand 2006). The concept of spatial structure as determined by the relative positions of organisms of different species (taxa) has already been discussed in the treatment of species associations, both pairwise and in the multivariate case in the use of 2^k tables to test for and document combinations of species that are unexpectedly rare or unexpectedly common (Chapter 2). In analysing species associations, location is defined by reference to the positions of individuals of a particular species, and the occurrence of other species in those species-defined neighbourhoods (however determined) are compared with expected values. While originally described for the analysis of pairs of species, there can be good reasons for extending the approach to examining sets of $k = 3, 4, 5, \ldots, s$ species, in which case 2^k contingency tables are required to detect rare

or common species combinations (Chapter 2 of this book).

Although the concept of ecological diversity originated with the underlying notion of the unpredictability of single species, the idea can be extended to the unpredictability of species assemblages, whether based on species combinations, lists of presences and absences, or on the species composition of collections, a vector of species quantities. Instead of measuring the diversity of *species* in a collection, therefore, we can measure the diversity (1) of the *species combinations* each represented by a vector of presences and absences, such as $\mathbf{p}_j = (1, 1, 0, 0, 1, \ldots)$, or (2) of the *species composition* at the different sites, each represented by a vector of species abundances, such as $\mathbf{a}_j = (10, 12, 0, 0, 3, \ldots)$. The former can be presented in schematic form by a diagram of sets of boxes, or of tally sticks, with filled units representing presences and empty units representing absences, as in Figure 10.9. Like these schematic diagrams of species presence and absence, in genetic studies similar diagrams of solid or hollow circles are used to show the presence and absence of haplotypes, but with links between them indicating unique mutational events (see Excoffier *et al*. 1992).

This approach may include an evaluation of how different the combinations are, or we may just count the different combinations that are present as all equal, without concern for similarity or complementarity. For example, for six species, the compositions (1, 1, 1, 0, 0, 1) and (1, 1, 1, 0, 1, 0) represent different combinations although they are quite similar (Figure 10.9, upper pair). On the other hand, (1, 1, 0, 0, 0, 1) and (0, 0, 1, 1, 1, 0) are absolutely complementary (Figure 10.9, lower pair), with 1s replacing 0s, and vice versa, and thus are as different as possible, but they might be counted just as two different combinations, equivalent in importance to the first pair.

The difference between combinations and compositions as the basis for sample diversity is that in the first case, we are concerned with identifiable sets of species in presence : absence data, for example species A, B and D, but not C or E, whereas in the second, we consider multivariate quantitative data.

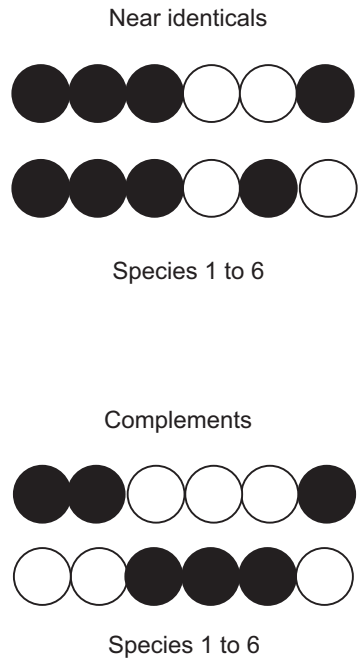


Figure 10.9 Presence (filled circle) and absence (open circle) for each of six species for two comparisons of composition. In the upper part, the two combinations are very similar; in the lower they are complements with presences and absences exchanged.

For the former, the number of possible species combinations is finite and the analysis is closely related to the mathematics of combinatorics; in the second, there are infinitely many, and the analysis is most easily approached by multivariate techniques such as ordination. The evaluation of both kinds of sample diversity, like that of species diversity, makes sense both at the level of a single collection (α), and at the level comparing several sites within a region (β).

10.3.1 Species combinations

Probably the easiest introduction to considering the evaluation of the diversity of species combinations is to start with the familiar assessment of the frequency

Table 10.4 Example of a 2 × 2 contingency table

Species A	Present	Absent	Total
Species B			
Present	a	b	$a + b$
Absent	c	d	$c + d$
Total	$a + c$	$b + d$	N

of pairs of species tending to occur together or not in spatial proximity as determined by sample units such as quadrats or in plotless sampling schemes such as nearest neighbours. For a pair of species, A and B, and given a sample of n quadrats, the number of quadrats which contain both species, the numbers with A but not B, B but not A, and with neither species are enumerated in a 2 × 2 contingency table, as here (Table 10.4).

Based on this table, a goodness-of-fit test uses the X^2 or G statistic and the χ^2 distribution to compare observed and expected frequencies, and a significant result is interpreted as indicating a positive association between the two species if $ad > bc$ and a negative association if $ad < bc$. In some cases, all pairs of species are tested to give an evaluation of $s(s - 1)/2$ possible pairwise associations, but there are problems with lack of independence for those tests (Dale *et al.* 1991). Knowing that the association of species A and B may be affected by the presence or absence of species C (and so on), an alternative to all pairwise tests is to evaluate the multispecies combinations using 2^k tables, where $2 < k < s+1$, and a goodness-of-fit test with the G statistic and $2^k - k - 1$ degrees of freedom. A significant result of the overall goodness-of-fit test can be interpreted using Freeman–Tukey standardized residuals for each cell of the table to indicate which cells, and thus which species combinations of presences and absences, are unexpectedly rare or unexpectedly common given the overall frequencies of the individual species (see discussion of this procedure in Bishop *et al.* 1975). Dale (1999) provided a discussion of the benefits and drawbacks of this approach, but one useful outcome is an accounting of the combinations that are rare and those that are common. These can be portrayed as vectors or as diagrams. For example, for six species, combinations such as (0,0,0,0,0,0), which has no species at all, and (1,1,1,1,1,1), which has all species present, may be very rare depending on spatial scale, whereas (1,1,0,1,0,1) or (1,0,1,1,1,0,0), which contain four species each, may be common or unexpectedly common. This approach is obviously very sensitive to scale in the sense of the grain determined by the size of the sample units, where larger units will contain more species on average.

Figure 10.10 (redrawn from Dale 1999, figure 5.8*c*) shows the 'significantly' high and low frequency combinations of eight species from SE Lyall moraines in the Canadian Rockies. Although 13 or so apparently significant results might be expected from randomness alone, the observed count of 35 is reassuringly larger than that, and we know that spatial autocorrelation in these data is not likely to have a large effect on the outcome (see Dale *et al.* 1991). The results are therefore likely to be a good indication of real effects in the community. The average number of species present is about the same in both categories (3.07 for high and 3.15 for low frequency combinations). There are no fully complementary combinations in these results (pairs with 1s exchanged for 0s and 0s for 1s) but combination H5 is a near complement of H13 and H15. The spatial relationship of complementary combinations may be of interest in the search for 'checkerboard' patterns of species occurrence. There are also a number of interesting 'reversals' where combinations with only two or three species present have an opposite frequency from more inclusive combinations that contain them (e.g. H3 versus L16 or L2 versus H9). We will not discuss this example in any greater detail, but it gives some idea of the kind of information available from this analysis. Clearly, however, association analysis using 2^k tables can reveal details about the spatial relationships of species not available from other methods. It is not that the pairwise analysis should be abandoned, because the overall association of two species, which the 2 × 2 tables represent, will be of interest and the 2^k method will often not be

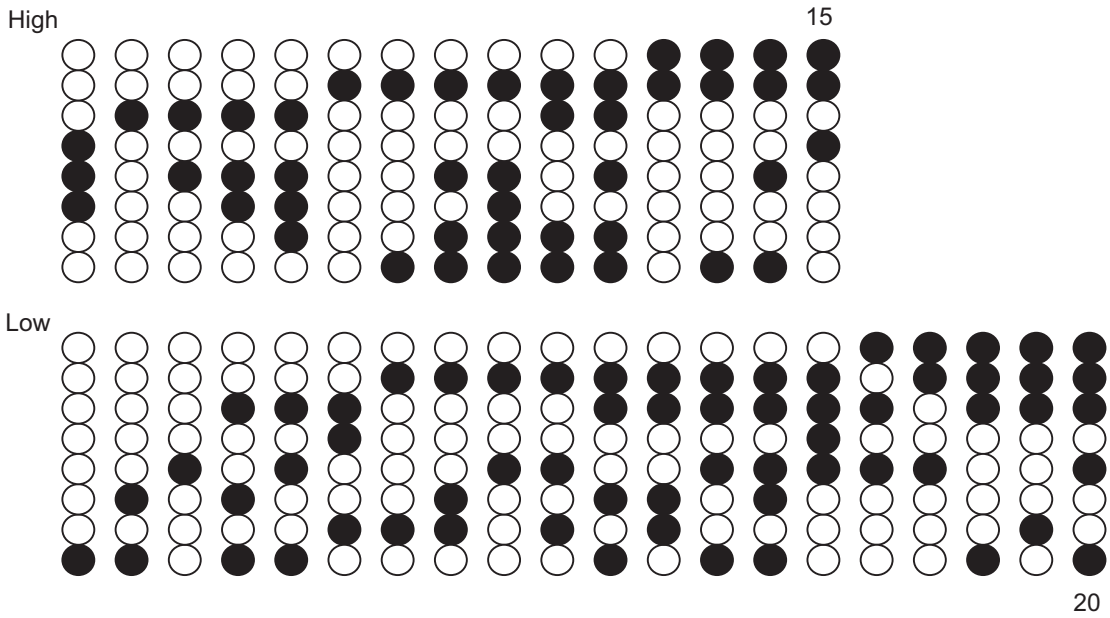


Figure 10.10 (redrawn from Dale 1999, figure 5.8*c*). Each column of eight circles represents the presence (solid) or absence (hollow) of each of eight species in a combination that occurs with significantly high (15 combinations) or significantly low (20 combinations) frequency based on the results of 2^k contingency table analysis. The data are from the SE Lyall moraines in the Canadian Rockies (Dale 1999).

tractable for large k unless n is very large, so that usually we will be addressing analysis for $k << s$. The details revealed by the multispecies method may prove useful, even if applied only to subsets of species that are most of interest.

We will end this section with a description of the approach used by Pielou & Pielou (1968) for testing when 2^k is large relative to the number of species. They studied 13 populations of the fungus found on dead birch trees in Gatineau Park, Québec, looking at the associations among the arthropod species (insects and spiders) inhabiting the fungal brackets as indicated by the lack of independence of their occurrence. Because their data were sparse and the number of cells in the 2^k table was large, problems with small expected values require an approach other than the 2^k goodness-of-fit test described above. Pielou & Pielou (1968) suggested two different test statistics: N_0, the number of brackets that are colonized, and C, the number of combinations of species present. The results of the tests were that N_0 tended to be somewhat less than expected (12 of the 13 populations), and that sometimes C was less than expected (clearly so in two populations and suspected in five more of the 13 populations). The authors commented that the evidence is that there were slight but real differences among the brackets in the probability that they were colonized, and that those differences were most likely due to the locations of the brackets, including their heights on the tree trunks. This approach may continue to be helpful in deriving information from sparse 2^k tables of species occurrences, but including the spatial information of location in the analysis from the beginning may increase its usefulness.

10.3.1.1 Combinatorial diversity

For the more general topic of the diversity of species combinations or *combinatorial diversity* for s species,

we begin with examples to illustrate the situation. Here two sets of eight samples, each with a total of seven species (Table 10.5). In the first example, there are eight different combinations of presences and absences, but only one instance of each.

The second example has only two distinct combination vectors (as given by the ordered entries in the columns), $\mathbf{v} = (1,1,1,1,1,1,0)$ and $\mathbf{v} = (1,1,1,1,1,0,1)$, but there are four instances of each. Suppose that the number of distinct combinations of the s species in the t samples is K, and the number of repetitions of the mth combination is κ_m so that $p_m = \kappa_m/t$. Using an information theoretic measure (like the Shannon–Weaver index, but with 2 as the base for logarithms), Juhász-Nagy (1993) introduced the following measure for the diversity of *combinations*:

$$F = -\sum_{k=1}^{K} p_k \log_2 p_k. \tag{10.15}$$

This was named the 'florula' diversity, because 'florula' is a diminutive of 'flora' indicating the combination of species present in a sample rather than what was found in a whole site or region.

The actual similarity of the combinations present in a set does not affect this calculation of diversity. This may seem to be a weakness, because two very similar combinations and two very different combinations count the same. In some circumstances, especially for a large number of species, it may be desirable to evaluate the observed combinations of species in a way that considers the similarity of the combinations, so that a set with four instances of the vectors (1,1,1,1,1,1,0) and (1,1,1,1,1,0,1) is considered to be

Table 10.5 Examples of different combinations of presences and absences

Set 1: Species × Samples ($H' = -\Sigma p_i \log p_i = 1.86$. $e^{H'} = 6.39$)

Samples:	1	2	3	4	5	6	7	8	∑
Species:									
A	1	1	1	1	1	1	1	1	8
B	1	1	1	0	0	1	1	1	6
C	1	1	1	1	1	0	0	1	6
D	1	1	0	0	1	1	1	1	6
E	1	0	1	1	0	0	1	1	5
F	0	1	1	1	1	1	0	0	5
G	1	0	0	0	0	0	0	0	1
∑	6	5	5	4	4	4	4	5	37

Set 2: Species × Samples ($H' = -\Sigma p_i \log p_i = 1.907$. $e^{H'} = 6.73$)

Samples:	1	2	3	4	5	6	7	8	∑
Species:									
A	1	1	1	1	1	1	1	1	8
B	1	1	1	1	1	1	1	1	8
C	1	1	1	1	1	1	1	1	8
D	1	1	1	1	1	1	1	1	8
E	1	1	1	1	1	1	1	1	8
F	1	1	1	1	0	0	0	0	4
G	0	0	0	0	1	1	1	1	4
∑	6	6	6	6	6	6	6	6	48

less diverse than one with four instances of combination vectors (1,1,1,1,0,0,0) and (0,0,0,0,1,1,1). Admittedly, in evaluating diversity at the level of taxonomic species, it is not usual to perceive greater diversity when the species are less closely related taxonomically, although that possibility does exist (Clark & Warwick 1998; Ricotta & Marignani 2007).

One approach for measuring combinatorial diversity is to calculate the similarity between vectors, for all pairs of combination vectors in a set. We can also summarize the information on combination comparisons by looking at the entries in a 2×2 contingency table for each pair of samples, or for each pair of species. The entries are the numbers of samples in which both species are present, a, and so on as in the contingency table (Table 10.4). Table 10.4 can give the Jaccard matching coefficient for the pairs of samples or the pairs of species, $a/(a + b + c)$, and the average coefficient for each set (Koleff *et al.* 2003; Legendre & Legendre 2012).

A logical extension of this approach is to consider a 2^s table that looks at the frequencies of all possible combinations of presence and absence of the s species simultaneously, rather than on the 'marginal totals' of pairwise summaries, as already described. In that treatment of the data, the table has s dimensions and each dimension of the table is associated with one species, like a coordinate axis taking values 0 and 1 for presence : absence data. For example, the data in Set 1, just given, would have eight entries in different cells of a 2^7 table that are 1, and a 0 in each of the remaining 120 cells. Set 2 gives a 2^7 table with two non-zero entries of 4, and the rest of the entries are 0. We can use the differences and similarities and the lack of independence among the observed combinations of species' presences and absences, to describe the concept of the 'effective number of combinations'.

This reference to 'effective number' has at least two precedents, one somewhat distant and one very close to the current topic. The more distant precedent is the development of methods to understand how spatial autocorrelation affects statistical tests (see Chapter 8). The presence of autocorrelation in data results in a sample of n observations which are not fully independent, having less information than a sample of n fully independent observations, potentially resulting in more apparently significant statistical tests than the data actually justify. By quantifying the lack of independence due to the autocorrelation, we can determine the 'effective sample size', n', which is the number of independent samples that contain the same amount of information as the set of n non-independent observations.

A closer precedent is the work by Hill (1973) on measures of diversity that can be seen as providing an estimate of the 'effective number of species' present (MacArthur 1965). In essence, one of the indices Hill (1973) suggested, $N_1 = e^{H'}$, determines the 'effective number of species' as the number of species that would provide the same diversity, as measured by the Shannon–Wiener information theoretic index, H', if they were all equally represented (i.e. with perfect evenness). In a similar spirit, Jost (2007) suggested that a true measure of β-diversity for N sites will produce the value N if the samples have no overlap at all in composition and the value 1.0 if they all overlap completely, giving a β-diversity index that is the 'effective number of distinct communities'. Jost (2007) gave the technical details of this suggestion, but one implication is that the 'currency' of β-diversity is different from that of α-diversity, being measured in 'communities' rather than in 'species' equivalents. (Although if we equate the unit 'community' with the average number of species in each one, a 'community' becomes defined simply as α species, just as β-diversity (in the sense of species turnover) is sometimes measured as a *Gleason* or a half-change, which could then be equated with α/2 species...) As a slightly more distant source of the concept, in the field of genetics, similar measures are found, such as the 'effective population size' (Wright 1931), the 'effective number of alleles' (Kimura & Crow 1964), and the 'effective number of codons' (Wright 1990). These are not as different as they might seem at first because the intention is to account for the lack of independence.

For species combinations, the effective number is the number of possible fully independent combinations

that the t non-independent combinations represent. The aim therefore is to evaluate the equivalent number of independent combinations, t', for any set of t combinations. The preceding discussion on representing presence : absence data in a 2^s table suggests that the maximum number of independent combinations is s. A sample set that contains all 2^s possible combinations of presences and absences, has only s that can be independent, so that $t' = s$, even if t is considerably greater. A set that has only two combination vectors, as does our Example Set 2 (Table 10.5), if they are independent, has $t' = t = 2$. To be most useful, a measure of the effective number of combinations should take into account both the similarity of combinations represented in a set of combinations and also the unevenness of their representation within the set. As for Hill's (1973) $N_1 = \exp(H')$, for the effective species number, the more equal the frequencies in a given set, the greater the effective number. Based on this thinking and on Hill (1973), we can suggest that where H is an entropy measure of the diversity of species combinations, then $M_1 = e^H$ will provide an estimate of the effective number of combinations.

From somewhat different starting points, the contributions of Ricotta (2006) and Jost (2006) came to a similar conclusion when their results are combined. To account for similarities or differences among the combinations in the data, Ricotta (2006) suggested modifying Juhasz-Nagy's florula diversity which is based on p_k, the relative frequency of the kth combination vector in the data, using some measure of the dissimilarity of the mth and kth such vectors, d_{mk}:

$$F = -\sum_{k=1}^{K} p_k \log_2 \left(1 - \sum_{m \neq k}^{K} d_{mk}\, p_m\right). \tag{10.16}$$

Jost (2006) extended Hill's (1973) suggestion for effective species numbers to a general contention that the exponential form of many familiar entropy-based diversity indices provide better measures of the true concept of diversity as 'effective number'. Combining the two ideas, and using the Jaccard coefficient as the basis for combination dissimilarity, we can produce a measure of the effective number of species combinations as M_1:

$$F' = -\sum_{k=1}^{K} p_k \log_e \left(1 - \sum_{m \neq k}^{K} [1 - J_{mk}] p_m\right) \text{ and} \tag{10.17}$$

$$M_1 = \exp(F'). \tag{10.18}$$

Analogs of other Hill diversity numbers, N_0 and N_2, are also possible, of course, but for our purposes the intermediate form seems the most appropriate. As deemed desirable, this measure is responsive to both the similarity of the combinations represented and the equality of their representation in the data set.

10.3.1.2 Examples of combinations of species presences and absences

Of the examples described above (Table 10.5), Set 1 gives $M_1(F') = 1.72$; Set 2 gives $M_1(F') = 1.16$, because the combinations are so similar. Set 3 (Table 10.6) gives 1.5, which is between 1.0 and 2.0 as suggested. As a final example, Set 4 (Table 10.6) illustrates the property that species diversity and combinatorial diversity are quite independent; here $N_1 = 4.94$ but $M_1 = 1.85$.

We may want to partition the diversity of species combinations into those parts attributable to within-site and to between-site variability. Because of the mathematical properties of their formulation, this partition is possible for F' by subtraction, with $F'_{\text{between}} = F'_{\text{total}} - F'_{\text{within}}$ and for M' by division: $M'_{\text{between}} = M'_{\text{total}} / M'_{\text{within}}$. Either will produce the same answer for the same data.

This 'effective number of combinations' evaluation of the diversity of species combinations clearly has many features to recommend it: simplicity, a close relation with other concepts of effective numbers, a close relationship with measures of species diversity, and responsiveness to both combination similarity and the equality of combinations' frequencies in the data.

Table 10.6 More examples of different combinations of presences and absences

Set 3: Species × Samples ($H' = -\Sigma p_i \log p_i = 1.055$. $e^{H'} = 2.87$)

Samples:	1	2	3	4	5	6	7	8	$\sum$
Species:									
A	1	1	1	1	1	1	1	1	8
B	0	0	0	0	1	1	1	1	4
C	1	1	1	1	1	1	1	1	8
$\sum$	2	2	2	2	3	3	3	3	20

Set 4: Species × Samples ($H' = -\Sigma p_i \log p_i = 1.597$. $e^{H'} = 4.94$)

Samples:	1	2	3	4	5	$\sum$
Species:						
A	1	1	1	0	0	3
B	1	1	0	0	1	3
C	1	1	1	1	0	4
D	1	1	1	0	1	4
E	1	0	1	1	0	3
$\sum$	5	4	4	2	2	17

Although we have mentioned that the initial information-theoretical method took no account of the similarity of the combinations, it is also true that neither approach (the entropy measure and the effective number transformation) take account of the relative locations of the combinations as they are observed. That is: it is not spatial. The locations of particular species combinations and the relationships between them become particularly important when the study of combinations becomes refined to the combinatorics of species co-occurences (nonrandom versus random) as applied to the assembly of communities (Connor & Simberloff 1984; Grant & Schluter 1984; Gotelli 2004; and many others). There are at least two kinds of nonrandomness to be considered: the nonrandomness of the combinations observed, and given that, the nonrandomness of their locations (leading to more hierarchical analysis!). The topic of the spatial structure of combinatorial diversity will wait, but some comments on compositional diversity are needed before that.

10.3.2 Comments on species compositional diversity

The diversity of combinations is based on vectors of s 1s and 0s, indicating the presence and absence of the s species, which can be summarized in a 2^s contingency table. In contrast, compositional diversity uses species densities or abundances, and the composition of a collection of sites can be depicted as a point in an s-dimensional space, with compositional diversity being some measure of the size and variability of a cloud of such points for all the sites under consideration. Then the analysis may include positive and negative correlations among species densities, or the tendency of identifiable groups of species to interact together. Because the occurrence of species and their abundances, when they do occur, are not likely to be independent, the points are not expected to be uniformly or randomly arranged in this multidimensional space. This leads fairly naturally to the concept of reducing the number of

dimensions needed to represent the essentials of the data using some ordination procedure.

The distinction between diversity of combinations and the diversity of composition can be confusing, because different authors use the terms in different ways. (For example, Juhasz-Nagy's paper on the florula approach to *combination* diversity is titled 'Notes on *compositional* diversity'.) To avoid confusion, we should reserve 'compositional diversity' for measures of the unpredictability of the set of species abundances of a spatially defined area, even if abundance is frequency: the number of small sampling units (quadrats, traps, point samples) in which the species is found. Given that restriction, compositional diversity becomes just another version of the range of concepts covered by the broad umbrella of β-diversity: here the differences in species composition among samples or sites. This leads naturally to a comparison of the differences in species composition between sites to the spatial relationships of those sites, as we will describe in greater detail below.

10.3.3 Nested subsets, constraining compositional diversity

10.3.3.1 Compositional agreement and complementarity

The concept of diversity is one of unpredictability, and one obvious aspect of the unpredictability of species assemblages is the relationship between the frequencies of given species and the overall richness of the collections in which they occur. One restriction on this relationship is the concept of nestedness or nested subsets. The concept is simple: rare species occur at few sites and only at the richest sites, so that the species-poor sites contain only the most common species. The species compositions at depauperate (species-poor) sites are therefore proper subsets of those of richer sites, producing nested subsets of species. There are a number of factors that can contribute to this observed pattern, but the theory of island biogeography suggests that if the sites are islands or at least insular, the size of the islands will have its strongest effect through the process of extinction, whereas isolation from a 'mainland' source of colonizers will have its greatest effect through colonization rates. Other factors, such as nesting of suitable habitat and passive sampling effects, may also play a role, but a number of studies have looked at the influence of isolation on nestedness structure, and isolation is a spatial factor, whether implicitly or explicitly so (Lomolino 1996; Davidar *et al.* 2002; Heino & Muotka 2005; McAbendroth *et al.* 2005; Feeley *et al.* 2007; Murakami & Hirao 2010). In the case of the last cited study, the authors examined the factors influencing nestedness in the insect fauna on small Bahamian islands. Spatial measures related to isolation that they used included distance to the mainland, over-water distance to mainland, distance to the nearest neighbour island and total area of neighbour islands within one of three threshold distances (250 m, 500 m and 1000 m). The groups Diptera (125 species on 28 islands), Lepidoptera (28 species on 26 islands), and Hymenoptera (55 species on 23 islands) all showed significant effects of at least one of the spatial variables on the observed nestedness. Therefore, while Simberloff & Martin (1991) may have been correct in their assertion that we do not expect extinction and colonization to produce characteristically different sets of nestedness scores, we may expect that the two processes have different spatial signatures (Darlington 1957; Lomolino 1996).

This phenomenon of nestedness is orderly because it produces more predictability than the random assignment of species to sites, no matter what determines site richness, and it therefore represents a restriction on compositional diversity. The usual way of depicting this relationship is by a grid of presences (1s) and absences (0s), with species ordered from most common to most rare, and sites from species rich to species poor (Figure 10.11). If the nestedness is perfectly ordered, the presences will be neatly packed into the top left part of the diagram, with the shape of the all-presence block being determined by the numbers of sites (m), species (s), and occurrences (P); see Attmar & Patterson (1993) and Ulrich *et al.* (2008). Departures from this perfectly ordered

(*a*) Perfectly nested: nestedness discordance = 0.

Sites / Species	a	b	c	d	e	f	g	h	i	j	k	l	Frequency
A	1	1	1	1	1	1	1	1	1	1	1	1	12
B	1	1	1	1	1	1	1	1	1	1			10
C	1	1	1	1	1	1	1	1					8
D	1	1	1	1	1	1				0			6
E	1	1	1	1					…				4
F	1	1						0					2
Richness	6	6	5	5	4	4	3	3	2	2	1	1	Σ = 42

(*b*) Less nested: nestedness discordance (1s below 0s in upper triangle) = 7.

Sites / Species	a	b	c	d	e	f	g	h	i	j	k	l	Frequency
A	1	1	1	1	1	1	1	1	1	1	1	1	12
B	1	1	1		1	1		1	1	1			8
C	1	1	1	1	1		1	1					7
D	1		1	1	1	1			1				6
E	1	1	1	1			1						5
F	1	1				1					1		4
Richness	6	5	5	4	4	4	3	3	3	2	2	1	Σ = 42

Figure 10.11 Nested subsets. (*a*) Completely nested with presences (1s) in the upper left of the diagram, and absences (empty cells, often depicted as 0s) in the lower right. The shape and position of the separation between the presences and absences will change with the number of species, number of sites, and their ratio. (*b*) Imperfectly nested with 'unexpected' presences or absences intermingled with the expected: some presences in the lower right and some absences in the upper left of the diagram.

nestedness appear as 'unexpected' absences in the block of presences in Figure 10.11 or as 'unexpected' presences in the block of absences (see part (*b*) of Figure 10.11). The determination of what is really unexpected can be in reference to the complete randomization of the P presences or by a restricted randomization in which the frequency of each species, p_i, is maintained and presences assigned to sites by probability weightings.

The causes of a nested subset pattern can be related to the total area available to the community, the range of substrates or the range of environmental conditions, the species' responses to factors that determine extinction, and the characteristics of the site that affect establishment or recolonization, such as island size, distance from the mainland source of colonizers, and isolation from other islands. If rare species are found only at sites with the most 'room' or the greatest range of conditions, they will be associated with the most species-rich communities and the nested pattern is found. On the other hand, the most environmentally limited sites

will have increased extinction rates of the most vulnerable species. In this explanation, there is no spatial effect in that there is no spatial relationship required between species-rich and species-poor sites or between sites of the same richness. Nor is there any requirement for assumptions about the dispersal of species or autocorrelation of their occurrences at neighbouring sites. Whatever the cause, the result is a non-spatial pattern of greater compositional agreement with species composition at least partly predictable from site species richness. The spatial aspects of nestedness patterns will be most evident when the driving forces are spatially 'contagious', whether through the dispersal of the organisms themselves, with different species having different abilities for movement and subsequent establishment, or through the spatially dependent movement of agents of extinction such as generalized predators or particular diseases. In those cases, the spatial pattern of nestedness will have a spatial signature of its own that we can assess using spatial analysis.

An alternative pattern to nestedness for presences and absences distributed over sites is the 'checkerboard' arrangement (that sounds spatial, but it is not always so), by which species exclude each other from sites by competition, perhaps in pairs of those most functionally similar. If this were a general rule, the species compositions of sites would be more complementary than would occur from randomness alone and the number of high frequency species combinations in a 2^k analysis that were complements or near-complements (as described above) would exceed expectations. If there were a spatial effect to the checkerboard, the expectation would be that adjacent sites would be more different than expected, with an alternation of 'black' and 'white' squares, whatever complementary combinations those labels represent, (species list A and the list ~A, in which all presences are replaced by absences and vice versa), producing the equivalent of negative spatial autocorrelation between the most closely neighbouring sites. Similarly, a spatial effect acting on whatever processes give rise to the nested subset phenomenon should make itself visible through the relative nesting patterns on near and far neighbouring sites, as we will investigate in a later section.

In some communities, it is possible to observe what is described as 'anti-nestedness' in which species from depauperate communities (those with few species or low diversity) do not occur in richer communities (e.g. ectoparasites on marine fish; Poulin & Guégan 2000). It is not clear, however, what complete 'anti-nestedness' should look like because while perfect nestedness is easily understood, see Figure 10.11*a*, there is no single opposite arrangement of presences in a site × species array (Almeido-Neto & Guimaraes 2007). On the other hand, it is clearly possible for a single site to exhibit an order of species abundances that is opposite to that in the entire set of sites under consideration, so that the entire set is somewhat nested, if imperfectly so, but the discordant site is clearly 'anti-nested' in the context of the other sites.

Beyond the simple contrast between 'nested' and 'not nested', there are clearly degrees of nestedness possible for any species × site table of presences and absences, and a number of methods have been proposed to calculate an overall nestedness measure (see Patterson & Atmar 1986; Wright & Reeves 1992; Almeido-Neto et al. 2008; and many others). The basic idea is to calculate the probability of the observed number of unexpected presences and unexpected absences, based on the observed species frequencies in the data. In practice this can be done in several ways, based on the null hypothesis that is most appropriate for the concept being tested. Most of the evaluations proceed by some kind of restricted randomization procedure; for example, the species frequencies are held constant and the presences are redistributed among sites with probabilities determined by the sites' values of richness, or vice versa with the site richness values held constant. The degree of disorderliness (away from a perfectly nested structure) is sometime conceived of as 'temperature' analogous to the increasing disorderliness of molecules as the temperature rises (Patterson & Attmar 1986). This analogy may be somewhat misleading because changes beyond pure randomness can lead to greater, rather than less, nestedness. On the other hand, we can apply the concept to a set of sites and

Box 10.1 Site nestedness scores

Presence : absence data for sites
Wilcoxon two-sample test statistic, U, based on ranks sum R; site score, $v_U = U/ n_1 n_0$, runs from 0 to 1.
Presence : absence data for sub-sites (gives site frequency data)
Count rank discordances: D; D_{max} is $s(s+1)/2$.
As a site score, $v_D = 1 - D/D_{max}$ runs from 0 to 1.
Abundance data at sites
Pearson's correlation coefficient serves as measure of similarity, and then the site score of $v_r = (r + 1)/2$ runs from 0 to 1.

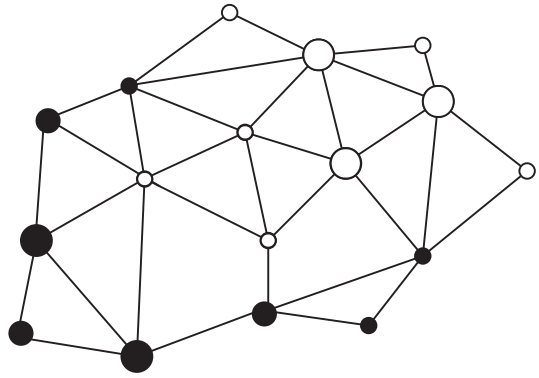


Figure 10.12 An artificial example of nestedness scores for sites (size = magnitude; black for high values, close to 1, white for low values, closer to 0), depicted as nodes of a spatial graph. The edges provide a neighbour network.

give each site a nestedness score, based on the concordance between the ranking of species abundances at the site with the ranking of species frequency or of total abundance over the entire set of sites. The exact nature of the measure used will depend on the data available, whether there is only presence : absence data for each site; sub-site presence : absence data, giving frequency data for each site; or abundance data for each site. Depending on the data, different measures of correlation or concordance with the overall species order can be used to evaluate the agreement of any site with the overall nested structure. Box 10.1 gives the details of three ways of creating a site nestedness score depending on whether the data are (a) site presence : absence, (b) site frequency data based on occurrence at sub-sites, and (c) site abundance data. The site nestedness score, thus derived, can be colour-coded for other purposes such as mapping and subsequent spatial analysis, with blue for cold, indicating high agreement with the overall ranking, and red for hot, indicating strong disagreement with the overall ranking; or the site nestedness score could be indicated by a spatial bubble plot with circle size representing magnitude with filled with black for good agreement and hollow (white) for poor agreement (Figure 10.12).

In the same way, a nestedness score for each species or for each site can be calculated by measuring the concordance of an abundance ranking with the overall frequency ranking (Simberloff & Martin 1991). Similarly, the degree of nestedness of groups of species or groups of sites can be assessed using an approach like Fisher's method (Fisher 1935, 1970) to combine individual probability values. More important, building on the concept of a spatial graph, as described in Chapter 3, a relative nestedness score can be derived for each pair of sites, so that in a spatial graph with the sites as nodes (each with a weight of its nestedness score), the edges between neighbouring sites can have its own weight of that measure of relative nestedness of the pair (as in Figure 10.13). A simple measure is an asymmetric matching coefficient: (matching presences less non-matched presences at the site with fewer species) divided by the number of species at that site. This is explained in Box 10.2.

Based on the evaluations for sites and for pairs of sites, we end up with a spatial graph for nestedness, with the sites as nodes and the edges showing the topological or functional neighbours among the sites. Each node has a nestedness score that is a measure of its nestedness compared to the whole set. Each edge has a score that measures the relative nestedness of the pair of sites. We can then use spatial clustering or boundary detection to delimit regions or sets of sites that are different in their nestedness characteristics,

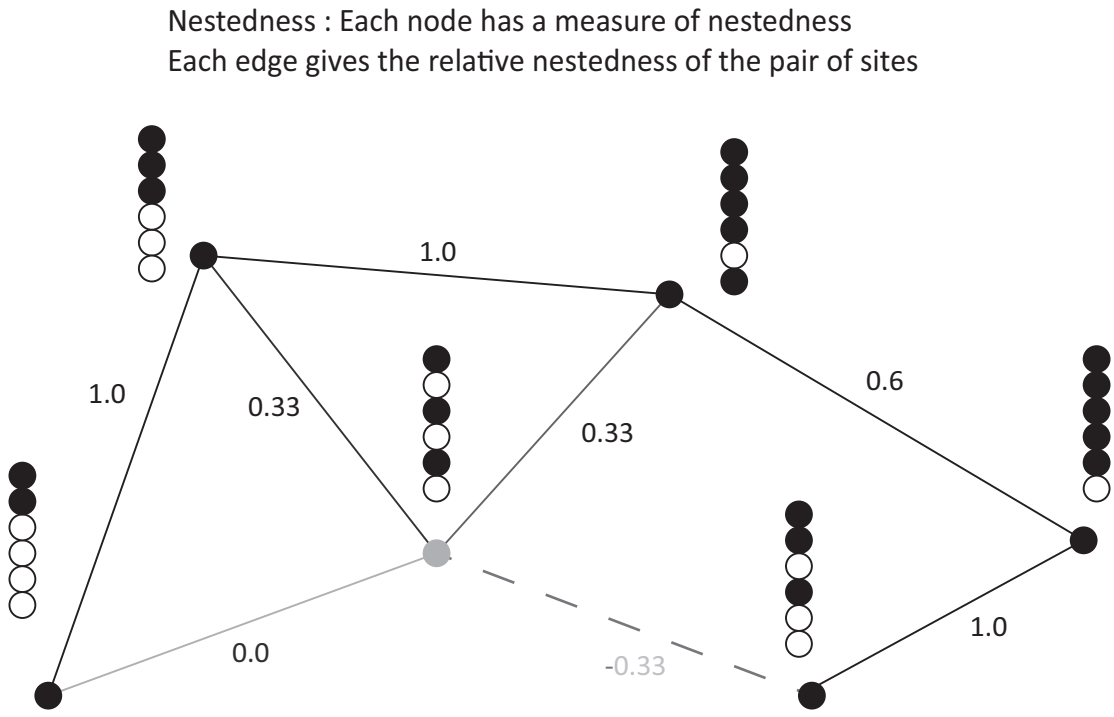


Figure 10.13 Weights on the edges of a spatial graph (the nodes are sites), giving the relative nestedness scores of neighbour sites. The edge depicted by a broken line is the only negative value. Some pairs are perfectly nested with a weight of 1.0.

Box 10.2 Measures of relative nestedness for pairs of sites

Unequal site richness

With a_{ij} as the number of species at the poorer site i also occurring at site j, $s_i < s_j$, and b_{ij} as the number at site i not at site j, a measure of relative nestedness is $m_{ij} = (a_{ij} - b_{ij})/s_i$, where m_{ij} takes values between -1 and $+1$

Equal site richness

For $s_i = s_j$, the measure is a symmetric matching coefficient of presences.

With a_{ij} and b_{ij} as for the unequal case, because $s_i = s_j$,
$a_{ij} = a_{ji}$ and $b_{ij} = b_{ji}$.
A measure of relative nestedness for sites of equal richness is $m_{ij} = m_{ji}$ as defined above, where m_{ij} takes values between -1 and $+1$

based on either set of scores or on both. The score map may also be used for other purposes, such as determining 'hot' or 'cold' regions of nestedness, with anomalies representing areas for the focus of conservation efforts or for further research on contributing processes.

There is obviously a close relationship between the concept and detection of nestedness in community composition and spatial analysis, despite the fact that the initial development of the nestedness concept was aspatial. It is also obvious that this is an area of spatial theory and spatial analysis in which there is more work to be done in developing methods and refining interpretation.

In the 'non-spatial' version of this discussion, we alluded to the concept of nestedness as an important characteristic of communities with overlapping species lists. Much of the interest in this topic is related to issues of conservation. If the species-poor sites contain

only subsets of the species-rich sites, conservation priorities can be focused on the latter; if the species-poor sites have entirely or mainly different species lists, then the focus of conservation efforts must be more broad (Jacquemyn *et al.* 2007). So far, space does not need to be invoked, but, if a spatial context is now added, whether in the form of an environmental gradient or in the form of dispersal corridors for recolonization after local extinction, the discussion is greatly changed. For example, in a study of orchids on Réunion Island, Jacquemyn *et al.* (2007) found significant nestedness but only within altitudinal ranges, indicating the importance of the spatial context for interpreting the results of a nested subsets analysis. One question is whether deviations from nestedness at species-poor sites can be related to dispersal and the composition of neighbouring species-rich sites. What is the relationship between the degree of nestedness at any particular site and the composition or nestedness of neighbouring sites? For example, in reference to Figure 10.11*b*, can the 'unexpected' presence of species *D* at site *i* be explained by appealing to its presence at sites that happen to be nearby? In particular, we commented that the description of species complements in some cases of island or effectively insular structures as 'checkerboard' sounded almost spatial in its implications. The idea is that the compositions of islands are more complementary than random, with species composition on island 1 being set A, then the composition of island 2 is very much like the complementary set, set ~A. If we depict those two as tally stick diagrams, depending on species ordering, we get the beginning of something that does look like a checkerboard (Figure 10.14). So far this description is not spatial, but a spatially explicit checkerboard pattern would be one in which first-order neighbours in a spatial structure tend to have complementary species compositions. Figure 10.14 illustrates this concept because in part (*a*) the complementary compositions are rarely first-order neighbours, but in part (*b*) first-order neighbours are frequently complementary in species composition. The latter is spatially 'checkerboard' as well as compositionally.

The main reason for spatial analysis of nestedness is in an attempt to detect the spatial 'signatures' of the different events that can contribute to the nested phenomenon. Given an archipelago of uninhabited islands, sequential colonization by a set of species with different colonizing abilities will give rise to a pattern that is well-nested overall and has high neighbour nestedness. On the other hand, given an archipelago with all islands starting with the same large set of species with different vulnerabilities to extinction, the resulting pattern will be well-nested overall if some sites retain most species, but neighbour nestedness will be low due to the spatial independence of extinctions. If there are many extinctions at all sites, all species lists may be small subsets of the original, and overall nestedness may be weak in addition to low relative nestedness of neighbours.

10.3.3.2 Examples of spatial analysis of nestedness based on published information

Example 1

Feeley *et al.* (2007) studied forest interior birds in recently isolated landbridge islands in Lago Guri, Venezuela (1986–2000).

There were 41 species on 26 such islands, most of which fall naturally into two groups: north and south. For this example, we used those two groupings, omitting islands 8 and 10, which lie between the two groups and are somewhat isolated from both. We also left out island 26 from the analysis, following the authors' advice and because it is an order of magnitude larger than the other islands (180 ha versus 23.3 ha, 14.7 ha, 12.3 ha, . . .).

Using this data set, we calculated nestedness based on order within the two groups of islands, rather than based on all the islands considered together (Figure 10.15). Three species were completely absent from the southern group.

Species richness is not significantly dependent on island size, but there is an obvious trend of lower richness on the smallest islands. The autocorrelation of species richness for first-order neighbours in the Minimum Spanning Tree is positive, but not significant.

There is positive autocorrelation in island area for first-order neighbours in the Minimum Spanning Tree.

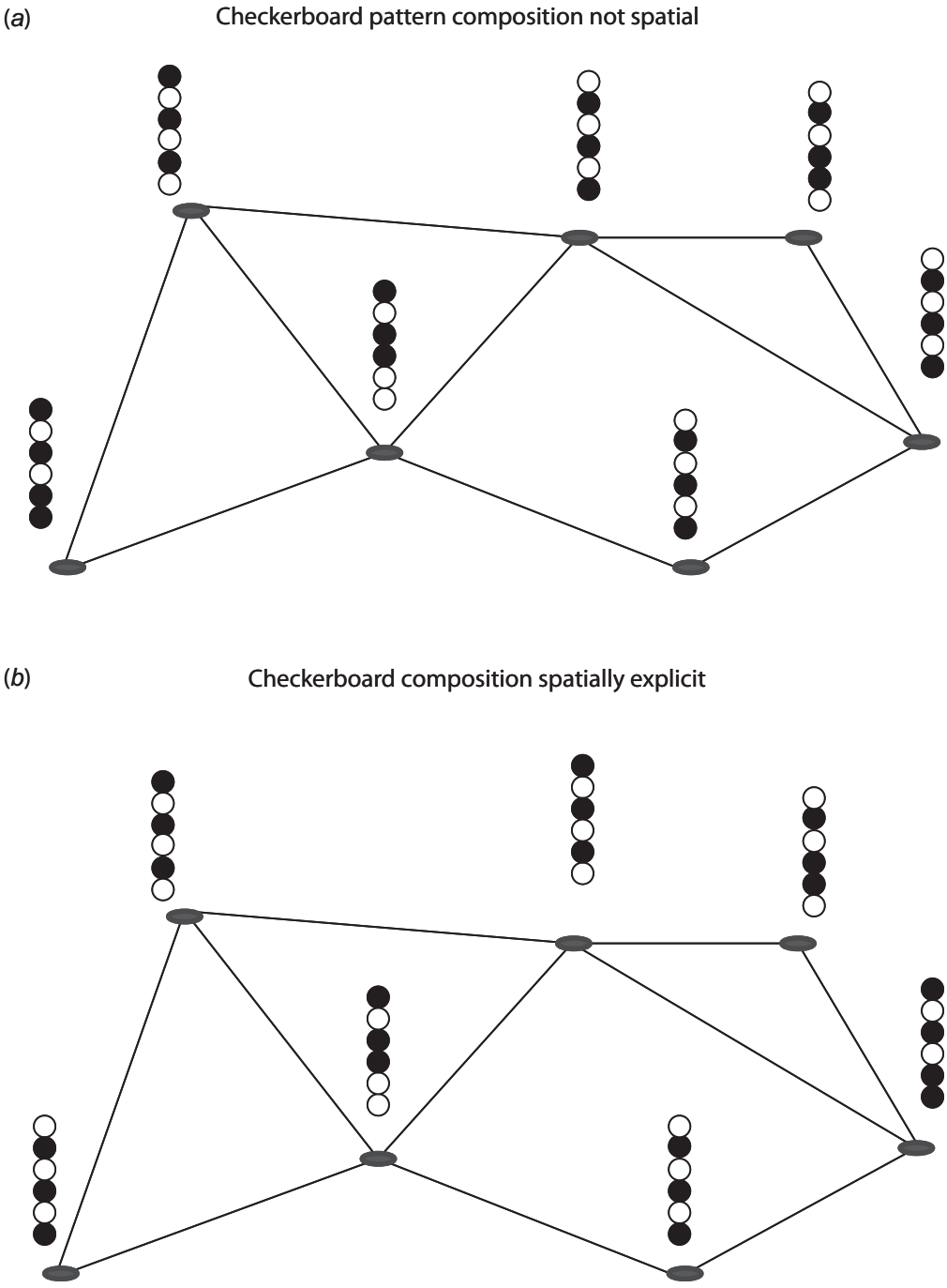


Figure 10.14 Tally sticks of species presence and absence, presented in a spatial graph indicating neighbours, where the patterns of presences and absences are like a checkerboard in being either very similar or mainly complementary. (*a*) Complementary patterns not adjacent (in fact, segregated), and (*b*) complementary patterns mainly adjacent, giving a spatially explicit checkerboard pattern of species presences.

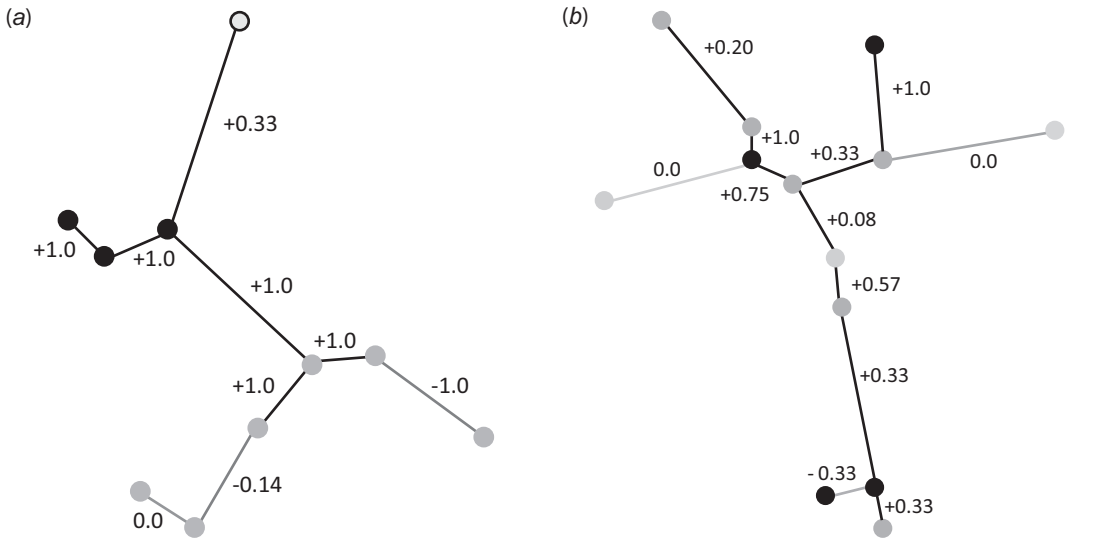


Figure 10.15 Spatial graph showing nestedness analysis for forest birds on Lago Guri islands (data from Feeley *et al.* 2007): nestedness scores for sites indicated by shading of nodes, relative nestedness shown by weights on edges. (*a*) Northern islands and (*b*) southern islands.

It is significant for the southern group and for both groups together, but not for the northern group alone.

Nestedness scores are not obviously predictable from island size, but two of the lowest nestedness scores are for the largest islands included. Those are regional nestedness scores.

Using the full data to create the scores, the lowest are for large islands, and for a small island with one species. Although the nestedness scores appear clustered in the northern group, and intermixed in the southern group (see Figures 10.15*a* and *b*), the autocorrelation of nestedness scores for MST neighbours in the northern group is actually negative and significantly positive in the southern group. Islands with similar nestedness scores can have low values of relative nestedness.

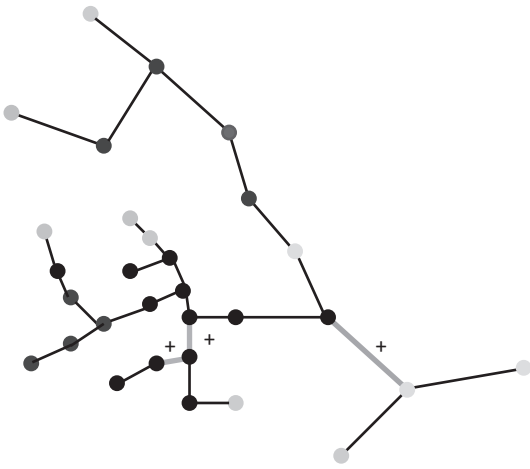
Example 2

Fattorini (2002) provided an interesting study of Tenebrionid beetles on islands in the Aegean.

There were 165 species on 32 islands, but we have omitted Crete (with 70 species) and Euboea (with 42), as being much larger than the others, and their species not found on other islands. That left 106 species on 30 islands, with richness ranging from 41 to 3.

Using this data set, we calculated a global nestedness score for all islands and the relative nestedness score for all pairs that were neighbours in a Minimum Spanning Tree.

Species nestedness is high and spatially organised with the highest nestedness scores clustered in the smaller islands in the south-central Aegean (see



All edges negative except three as indicated by the symbol '+'

Nodes coding: black = (0.90 - 1.0);
dark = (0.80 - 0.90); light = (0.50 - 0.80)

Figure 10.16. Spatial graph showing nestedness analysis for Tenebrionid beetles on Aegean islands (data from Fattorini 2007): nestedness scores for sites indicated by shading of nodes, relative nestedness of neighbours all negative except for the three labelled with plus signs.

bottom left of Figure 10.16). There is a trend to decreasing nestedness on the periphery. The relative nestedness of neighbours was low, almost universally, with the few exceptions noted in Figure 10.16. Part of the reason is that with many species and low island richness, there is a low probability of large overlap in the lists of neighbours, even if each list is well-nested.

We have a few comments on the approach for spatial analysis of nestedness described here.

(1) These comparisons should be informative even if the full data set is only poorly nested.
(2) Although there are choices for assigning site nestedness and concordance scores, the method will accommodate almost any that is 'well-behaved'.
(3) The spatial graph with the weights on nodes and weights on edges can be used to find spatial clusters and boundaries.
(4) The spatial 'signatures' of different mechanisms causing nestedness may not be as distinct as we would like.

This approach allows the identification of spatial signatures of causes of nestedness, and it allows the identification of clusters of sites or of regions delimited by boundaries with similar degrees of nestedness.

10.4 Multiple classifications

Another extension of the simplest forms of diversity analysis is to consider two or more criteria, or two or more levels, of classification of the organisms. For example, taxonomic classifications are hierarchical and so, in addition to calculating diversity based on species, a second level of diversity can be calculated based on genus, allowing a subsequent partition of species diversity into within-genus diversity and between-genera diversity. Clarke & Warwick (1998) have extended this idea to include the full taxonomic hierarchy (species, genus, family, order, ...) into a measure of diversity called a 'taxonomic distinctness index'.

It is also possible that the organisms are classified by two or more independent schemes, such as growth form and genus or family and status as native or non-native, in which case each organism is treated by two different classifications.

Given two classification schemes of the same objects, call them C and G, the diversity based on joint classification can be partitioned as:

$$M(C\&G) = M(C) + M(G) \tag{10.19}$$

provided C and G are independent classification schemes, for example tree species and tree height (cf. Pielou 1975b). The diversity in the double classification is the sum of diversity based on classification C and the diversity based on classification G. Under those conditions, the relationship is more properly:

$$M(C \times G) = M(C) + M(G). \tag{10.20}$$

The relationship is exact only when the classifications are statistically independent as well as biologically independent so that the proportions in the classes of C within each G-class are the same as in the overall data set.

If the classifications are completely dependent for a fundamental or biological reason, then

$$M(C \,\&\, G) = M(C) = M(G) \tag{10.21}$$

and

$$M_C(G) = M_G(C) = 0. \tag{10.22}$$

That is, the average diversity for classification C within subsets defined by classification G (and vice versa) is zero. The cross-classification scheme can become (almost) spatial if, for example, classification C is a taxonomic classification of species, and G is a classification of the sites by habitat type. Under those circumstances, as Pielou (1977b, chapter 19) points out, given the more usual situation of some intermediate level of dependence between the two classifications, both ratios $M_C(G)/M(G)$ and $M_G(C)/M(C)$ will take values between 0 and 1, and can be interpreted as measures of species 'niche breadth' in the first case (for example, low values indicate that each species tends to occur only in a small range of the habitats), and average 'niche overlap' in the second (high values indicate that most habitats contain a good representation of the species in the region).

For a hierarchical classification of C within G, as with species within genera, also with the assumption of independence, this becomes:

$$M(C \,\&\, G) = M(G) + \overline{M}_G(C). \tag{10.23}$$

Now, the diversity based on the double classification, which could be considered to be the total diversity, is the sum of diversity based on classification G and the weighted average diversity based on C within G classes. The relationship then becomes:

$$M(C \mid G) = M(G) + \overline{M}_G(C). \tag{10.24}$$

Because the structure is hierarchical, $M_G(C)$ makes sense as a quantity, but $M_C(G)$ does not.

Silvertown *et al.* (2006) provided an interesting example of including phylogeny in a study of plant diversity by comparing congeners and noncongeners in the spatial hierarchy of diversity: α, β, and γ. They found that some aspects of β- and γ-diversity reveal evolutionary conservatism in the similarity of traits as revealed by habitats (β) and geographic ranges (γ).

In another approach, using a taxonomic hierarchy with more than two levels, Clarke & Warwick (1998) provided a technique that calculates a diversity index using a series of taxonomic distances:

0 = same species,
1 = different species in the same genus,
2 = different genera in the same family, and so on.

It is essentially a measure of the average taxonomic distance between species, weighted by their abundances. Where n individuals have been observed, and there are x_j of species j, with the taxonomic distance between species i and j being w_{ij}, the measure is:

$$\Delta = \frac{\sum_i \sum_{<j} w_{ij} x_i x_j}{n(n-1)/2}. \tag{10.25}$$

When all the distances are 1, this reverts to a version of Simpson's index:

$$\Delta_{\equiv 1} = \frac{1 - \sum_i (x_i)^2}{1 - 1/n}. \tag{10.26}$$

The authors also introduced

$$\Delta^* = \frac{\sum_i \sum_{<j} w_{ij} x_i x_j}{\sum_i \sum_{<j} x_i x_j}, \tag{10.27}$$

which is the expected distance between randomly chosen individuals that are not of the same species. For presence : absence data, the measures become

$$\Delta^+ = \frac{\sum_i \sum_{<j} w_{ij}}{s(s-1)/2}. \tag{10.28}$$

What is being measured by these indices is a 'distance', whether it is taxonomic or otherwise, and the units of the measure will be the same as the units of distance. There is no reason to suppose that the distance used could not be actual spatial distance between objects instead of taxonomic distance.

When the concept of using more than one classification scheme was introduced, there was a distinction made between situations in which the classifications were hierarchical (e.g. classification by species is contained within classification by genus) or more-or-less

independent, producing a cross-classification scheme (e.g. tree size by tree species). The difference between the two cases becomes amplified when we consider a spatial context. When the double classification is hierarchical, the interaction of the spatial structure with one of the classification schemes cannot go beyond the interaction with the second (nested) classification. However, when the classifications can be independent, there is a range of interesting possibilities for spatial structure to interact with them. Examples may be found in ecological genetics or landscape genetics, where genetic diversity is measured on potentially independent components. For example, Bourobou *et al.* (2010) in a conservation study of the Moabi tree (*Baillonella toxisperma*, Sapotaceae) in Central Africa, used microsatellite markers to examine the spatial genetic structure of the population. They looked at relatedness as a function of distance for both nuclear and chloroplast microsatellites and found that these gave very different results, indicating greater limitations on seed dispersal (chloroplast markers = maternal) compared to pollen (nuclear markers).

In another study of tropical trees, Ng *et al.* (2004) looked at the spatial structure and genetic diversity of two species of *Shorea* (dipterocarp), using four allozyme loci and seven microsatellites. They also divided the trees into three diameter classes for analysis and used a version of Ripley's K analysis to evaluate the spatial pattern of the stems. They observed stronger spatial structuring in the smallest diameter classes of both species in part due to limitations on seed dispersal in both species. Dufresne *et al.* (2002) also compared allozyme and microsatellite markers in an explicitly spatial study of the barnacle, *Semibalanus balanoides*, in the region around the Gulf of St. Lawrence to detect geographical shifts in allele frequencies near the Miramichi River. (They provided a map of the allele frequencies at two loci which could be used as a spatially explicit example, although they did not do the full spatial analysis.) In this kind of example, with two potentially independent classifications, a spatial analysis of the cross-classified data has the potential to be highly informative. This is another area of analysis where there is much room for further developments.

In research in molecular ecology and spatial genetics, the technique of analysis known as Analysis of Molecular Variance (AMOVA) has been gaining popularity since it was introduced by Excoffier *et al.* in 1992. This analysis technique is hierarchical like the familiar nested Analysis of Variance approach, examining the variation among individuals within populations and populations within regions, and partitioning the associated variation by level. Although not explicitly spatial, this technique for partitioning genetic diversity can be easily placed in a spatial context and the final analysis and interpretation adjusted accordingly. For example, the results could be mapped or further analysed for evidence of isolation-by-distance (see Rousset 1996). As further developments, Doupanloup *et al.* (2002) have provided the basis for a spatial version of the method, known as SAMOVA, and Jombart *et al.* (2008) describe a spatial principal components analysis (sPCA) to elucidate the spatial structure of genetic diversity.

We will not pursue this extension from the basic concept of diversity much further here, but it may find an important application in studies related to extinctions and the preservation of biological diversity in its broadest sense. There are probably important spatial components to this kind of analysis, but those have yet to be worked out fully or applied to available data. One interesting area of study that would require this kind of analysis would be to combine biogeographic, phylogenetic and ecological information to investigate how patterns of biological and taxonomic diversity are embedded in environmental and large-scale dispersal structures (e.g. Westoby 2006).

A good spatial application of this cross-classification approach can follow Pielou's (1977b) suggestion of using species × habitat classification, but making the classification species × location. For example, we can have the quasi-spatial analysis of species of epiphytes found at different locations on trees: base, trunk, large branches, small branches (Table 10.7), as follows.

$M(SL) = 2.41.$

$M(L) = 1.38;\ M(S) = 1.76.$

$M_S(L) = 0.65;\ M_L(S) = 1.03.$

$M_S(L)/M(L) = 0.472;\ M_L(S)/M(S) = 0.587.$

Table 10.7 Epiphyte species abundances by position on trees (artificial example).

Species	A	B	C	D	E	F
Location						
Base	48	30	12	0	0	0
Trunk	8	66	26	24	0	0
Large branches	0	0	10	30	32	24
Small branches	0	0	0	0	28	62

The relationship with the familiar goodness-of-fit G statistic is that:

$$G = 2n[M(S) + M(L) - M(SL)].$$

Here, $G = 800[1.76 + 1.38 - 2.41] = 584$.

With 15 degrees of freedom, the result is highly significant, and clearly the species differ markedly according to location. A more involved spatial analysis of diversity could include more 'dimensions', with a classification for x-location and y-location as well.

10.5 Spatial diversity: putting it all together with spatial graphs

One major conclusion from considering the spatial aspects of diversity analysis is that indices of diversity or measures of richness, being synthetic variables, can conceal much important information about the spatial relationships among samples, sites, or regions. It is easy to be tempted to make interpretations based on similarities in richness or diversity that really should be based on species composition (see Selmi & Boulinier 2001). For example, it is quite possible for sites that are spatial first neighbours to have similar diversity or richness, even though it is second-order spatial neighbours that have greater similarity of species composition. Figure 10.17 provides an artificial example that illustrates this point, using richness as a simple version of diversity. The majority of joins are between sites with the same richness (6 of the 9),

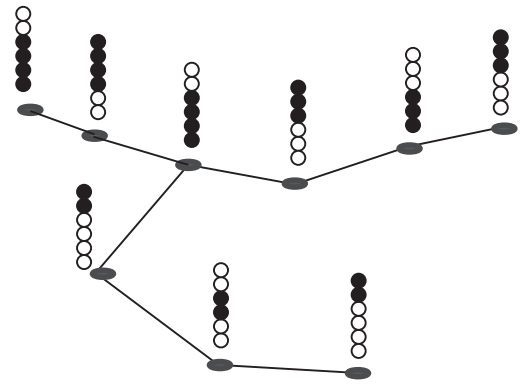


Figure 10.17 An artificial example showing high neighbour similarity in species richness, but first-order neighbours are quite different in composition; second-order neighbours are more similar.

but they are of low similarity (using Jaccard's index: 0/4, 0/6, or 2/6), and all uniquely second-order joins have a higher similarity (2/4). This point about indices is not new, but the inclusion of the spatial context as an explicit part of the analysis emphasizes the conclusion. A corollary, of course, is that the spatial component of the analysis of diversity may often be crucial to understanding the patterns that are present in the data. The converse is that if diversity were just a number, or a simple measure, then its spatial analysis would be the same as the spatial analysis of any quantity, with trends and spatial autocorrelation. It is the complexity of the factors that contribute to a measure of diversity that makes its spatial analysis interesting. That is also the explanation of why we spent so much space in this chapter on the basic analysis of species combinations and species composition diversity.

With that preamble, in the remainder of this section we will attempt to provide a synthetic guide to the spatial analysis of diversity, based on the use of spatial graphs, as described in Chapter 3. The starting

point is a set of sites with locations, each with a list of the species present, with or without some measure of the species' abundances. These can be analysed by themselves, by looking at composition or a measure of diversity as a function of location (latitude, longitude, altitude, distance from the ocean, etc.) or they can be analysed as the nodes of a spatial graph, with the edges to be determined in one of several ways (physical distance, topological considerations, functional connection, etc.). Whether formulated explicitly or not, the edges of the spatial graph essentially provide the definition of which pairs of nodes are considered to be neighbours, and so any analysis that involves neighbours or neighbourhoods moves into the use of spatial graphs. As a specific example, consider Shimatani's approach to spatial diversity analysis, given in Section 10.2.1.1, and which is closely related to Ripley's multivariate K described in Chapter 4: it evaluates the probability that two randomly chosen individuals within a given distance of separation belong to different species. That is exactly the same as taking the mapped locations of the individuals as the nodes of a spatial graph, and defining its edges and the nodes' neighbours by a threshold of the same distance as that being tested. That is, the method uses a distance-defined spatial graph, although at first glance it might appear that the method is based only on nodes.

We can summarize the approaches described in this chapter based on a number of different categories as applied to the creation and analysis of a spatial graph. The first category is a general description of the 'property' or ecological characteristic being investigated, including such things as neighbour diversity, diversity as a function of scale (Shimatani's K), spatial structure of richness or of diversity of species combinations, nestedness, and so on. The next category is the identity of the units that are nodes in the spatial graph: individual organisms, sites, or samples. Having identified the nodes, the next category is the rule used to determine which pairs of nodes are joined by edges. The range is large, from the 'empty graph' with no edges to a complete graph (or 'universal graph') with all pairs joined, but the most usual choices lie between the Minimum Spanning Tree (MST) and the Delaunnay triangulation (DT), with an average of about two and about six edges attached at each node (Chapter 3). Neighbour graphs that are sparser, such as a graph of nearest neighbours, are less useful in most situations because they are not fully connected. Another kind of rule to determine edges is to use a threshold value of physical distance and then to create an edge between any pair of points that are closer than that threshold distance. Both the nodes and the edges can have labels or weights associated with them, and so the next two categories for classification can be the node label, such as a site species richness value or a nestedness score, and the edge label, such as a comparison of species list similarity or the relative nestedness of two sites. We can also use some overall graph characteristic to describe the purpose of the analysis, for example the search for hot spots of the property being investigated or for regions of relative homogeneity using cluster identification or boundary detection. In many cases the evaluation of a characteristic will involve comparisons of indices, boundary or cluster detection, or the assessment of spatial autocorrelation as a function of distance whether in a physical measure or in path length within the spatial graph.

Box 10.3 uses these categories to provide a summary of the approaches and methods described in this chapter. As described in detail in Chapter 3, the comparison of the results from two graphs based on the same nodes, but with different edge rules, allows us to test different hypotheses about the forces structuring diversity in the system being studied. For example, if there is much greater similarity of species composition between pairs of first and second neighbour sites in a graph based on functional connections (e.g. river flow) than in a graph based on geographic distance, this provides good evidence of dispersal of the organisms by water rather than by air.

10.6 Temporal aspects of spatial diversity

Diversity can also be located or partitioned in time, but temporal partitioning is much less common in ecological studies, although it is a more frequent

Box 10.3 Summary of characteristics for diversity analysis with spatial graphs

Property	Node	Edge rule	Node label	Edge label	Graph character	Test procedure
Neighbour diversity	Individual	Any (DT)	Species	None	Species differences	Compare counts
Shimatani's K	Individual	Distance thresholds	Species	None	Diversity versus scale	Counts versus distance
Richness	Site	Any (DT) or complete	Site richness s_j	β_p (site pair beta diversity for p/a)	Richness variation Hot spots/ regions	Index; cluster or Boundary detection; sp.a.c. versus path length
1° diversity	Site	Any (DT) or complete	Site diversity M_j	β_d (site pair beta diversity for abundances)	Among site diversity Hot spots/regions	Index; cluster or Boundary detection sp.a.c. versus path length
Composition	Site	Any (DT) or complete	Tally stick p/a	Difference tally	Regions?	Clusters/boundaries sp. a.c. versus path length
Composition	Site	Distance thresholds	Tally stick p/a	None	Distance decay	Similarity versus distance
Combinatorial diversity	Site	Complete	Tally stick p/a	None	Florula diversity	Significance
Nestedness	Site	Any (MST, DT)	Site score	Direction & Relative nestedness	Hot spots/ regions	Clusters/boundaries sp.a.c. versus path length
Composition	Site	Functional connection (rivers, corridors,...)	Tally stick p/a Abundance vector	Direction (?)	Neighbour similarity	Similarity versus path length

p/a indicates presence : absence data.
sp.a.c. indicates that spatial autocorrelation coefficients are calculated and evaluated as a function of path length.
Column 1 is the ecological characteristic being investigated.
Column 2 is the identity of the units that are nodes in the spatial graph.
Column 3 is the rule used to determine which pairs of nodes are joined by edges. This can be a topological rule (e.g. Minimum Spanning Tree, MST, and the Delaunay triangulation, DT), a distance threshold rule, or the use of all edges to give a complete graph.
Column 4 is node label, which can be a value (e.g. species richness) or a complicated label (e.g. a species list depicted as a tally stick).
Column 5 is the edge label, e.g. similarity index of two sites or their relative nestedness.
Column 6 is the graph characteristic that is the focus of the analysis, e.g. detecting hot spots of a property, the scale of spatial autocorrelation, or homogeneous regions.

topic in evolutionary and paleontological literature (cf. Rosenzweig 1995). Temporal partitioning is not that different from spatial partitioning, sharing the difficulties of dealing with continuous variation that can be sampled at a range of different scales, depending on the sample 'window' or template that is used, and whether the templates are applied with overlap, contiguously, or with gaps between them. In ecological studies of plant systems, such as a study of community succession, it is much more common merely to track diversity as a function of time or site age, rather than partitioning total observed diversity into temporal subsets. There are many examples of this approach (Fortin *et al.* 1999; Huston 1994, chapter 9), but here we need to acknowledge that diversity is not a real property of the community; it is a derived variable that is a short-hand and imperfect summary of more complex characteristics of the community. Diversity is a measure, certainly, but we can get into difficulties, both conceptual and practical, if we start thinking that there is a something in the community called diversity that we should set out to measure. This is particularly true if we start thinking about the changes in this measure through time, as the components that contribute to changes in diversity themselves may change. Large changes in the species list may not be reflected in large changes in the diversity we measure. Similarity in diversity, say at the early and late stages of succession, may tell us nothing essential about the composition and functioning of the community (see Loreau 2010, chapter 3; for an interesting discussion of the relationship between diversity and function in ecosystems). Similarly, in comparing diversities, particularly when we want to compare the communities themselves, and especially when considering spatial relationships among those communities, we need to be cognizant of the fact that the component of diversity we call richness is also a derived variable based on species lists.

On the other hand, the derived or synthetic nature of the variable should certainly not exclude it as a characteristic of interest and interpretability, and as an important subject for study, particularly a study of its changes through time and the factors that seem to affect it. Similarly, other characteristics related to diversity, such as nestedness, are not static variables, and their dynamics should be investigated further. For example, in a study of the nestedness of archipelago floras in the Bahamas, Morrison (2013) found that nestedness changed little over time, despite changes in the species composition itself.

10.7 Concluding remarks

It is clear that the spatial analysis of ecological diversity is both a complex and interesting subject, and a key part of our understanding of ecological systems. It is an endeavour that is still, itself, too diverse, and more effort is required to achieve greater clarity. It is our belief (and hope) that including the spatial component will provide a clearer understanding of the phenomenon and its measurement, rather than adding greater complication. Of course, that may not be easy itself.

As suggested in the introduction to this chapter, ecology is not the only science that has puzzled over the concept and measurement of diversity and how its spatial aspects can be included. In particular, there has been much work done on spatial analysis in genetics (Vekemans & Hardy 2004; Jombart *et al.* 2008; Kelly *et al.* 2010), landscape genetics (Diniz-Filho *et al.* 2009), and phylogeography (Miller *et al.* 2006; Kidd & Ritchie 2006; Bloomquist *et al.* 2010). Escudero *et al.* (2003) provided a review of the more standard approaches in genetics (Mantel test, correlogram, join count autocorrelation). The application of variograms is described in Wagner *et al.* (2005), and point pattern analysis in Miller (2005). The more recent review by Guillot *et al.* (2009) covered some of the same material but focused on methods to detect the phenomenon of isolation by distance and on clustering methods.

Following this thought, we are reminded that the usual categories of species, or ecotype, or genotype, are not the only bases for the evaluation of diversity. Depending on the application, we might be interested in diversity based on the sizes of individuals, their

age, some classification by 'functional type', effective breeding system, or other characteristics that are affected or caused by interactions with the environment.

The final comment here follows the trend that shows up throughout this book, which is the recommendation that we have to move from analyses that consider only space to analyses that consider both space and time, whether it is the change in spatial measures through time, the dynamics of spatially explicit measures at individual locations, the spatial structuring of temporal statistics and temporal series, or measures and statistics that are truly spatio-temporal in nature.