Mapping variations in the strength and breadth of biogeographic transition zones using species turnover

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SUMMARY

Biogeographic regions are widely regarded as real entities, or at least as useful summaries of the complex patterns of spatial concordance among species. The problem is that, whereas some parts of the transition zones between regions may be strong and abrupt, other parts of the same zones may be weak or broad, so that the corresponding parts of border lines drawn on maps, although convenient, are arbitrary constructs. One approach to investigating transition zones ascribes values to the area units themselves, by quantifying the spatial turnover among species within the surrounding neighbourhoods of areas on maps. Using data for bumble bee distributions world-wide, I show that quantitative measures of neighbourhood turnover can discover many of the transition zones that are found by classification techniques when applied to the same data. But unlike classification techniques, turnover measures, particularly when used in combination, can show how a transition zone varies along its length, not only in its strength (the proportion of species contributing to the zone) but also in its breadth (the degree of spatial overlap or the degree of coincidence among species replacements across it). For bumble bees at least, these transition zones are also negatively associated with areas that have a combination of both high species richness and high species nestedness.

1. INTRODUCTION

Exploring biotic transition zones is an essential part of studying the processes that govern the distribution and diversity of organisms, and yet important aspects of the patterns of variation are not adequately described by existing quantitative techniques. For example, the ease with which classifications of biogeographic regions can be communicated and understood has made them popular descriptive summaries of biological distributions for over a century (Sclater 1858; Wallace 1876; Udvardy 1975; Groombridge 1992). More recently and at finer spatial scales, ecotones between landscape elements have become an important focus for studying environmental change (Holland *et al.* 1991; Hansen & di Castri 1992). But across this broad range of spatial scales, variation in the composition of species assemblages appears to 'hover tantalisingly' between the conveniently discrete and the more continuous (Clements 1916; Gleason 1939; Shimwell 1971). As a result, while transition zones may form strongly and sharply defined boundaries in some parts of their lengths, elsewhere they may be weak or consist of broad clines or gradients (usage of the terms 'boundaries' and 'clines' or 'gradients' to distinguish abrupt from more gradual cases of 'transition zones' follows Barbujani *et al.* 1989). Therefore, despite the complexity of available techniques (Gauch 1982; Hengeveld 1990), some parts of the border lines drawn on maps, however appealing, remain essentially arbitrary constructs (Peters 1955; Simpson 1977) (usage of 'border line' distinguishes the lines imposed on broad transitions by classification methods from any underlying, genuinely abrupt biological boundaries). As a first step towards understanding the historical and ecological processes that generate and maintain these different kinds of transition zones, in this paper I use measures of spatial turnover among species to map how the strengths of transition zones (the proportion of species contributing) vary along their lengths within broadscale data for bumble bees (this usage of 'turnover' for changes in faunistic or floristic composition, which may be qualified as relating to either temporal or spatial axes, follows for example Whittaker 1972; Wilson & Shmida 1984; Delcourt & Delcourt 1992; Harrison *et al.* 1992). Comparisons among the results of different turnover measures are used to gain additional information on the different breadths (the degree of spatial overlap or the degree of coincidence among species replacements) of transition zones.

Some previous studies of transition zones have begun with pre-defined border lines and have sought only to extract these from other information about land classes within the landscape, for example using techniques from image analysis (Johnston *et al.* 1992). Most previous approaches to quantifying transition zones using data for species have dealt with transects on a single spatial dimension (e.g. Whittaker 1960; Greig-Smith 1983; Wilson & Shmida 1984; Dale 1988; Orlóci & Orlóci 1990; Turner *et al.* 1991; Delcourt & Delcourt 1992). In extending this to surveys on two spatial dimensions, the simplest method has been to map the density of species' range-limits (see, for example, McAllister *et al.* 1986). The more elaborate methods to associate scores with area units (such as cells on maps partitioned by grids) may be divided into two groups, depending on whether the aim is to apply scores either: (i) to points or lines on grid-cell edges, as elements of a border; or (ii) to the area of each grid cell as a part of a transition zone, irrespective of breadth. If transition zones sometimes encompass more than one grid cell within their breadth, then choosing edge methods will constrain the results.

A popular approach for seeking border lines or edges in two-dimensional spatial data is to apply classification techniques. This provides some information on boundary variation, although it is limited to the relative strengths of entire border lines as represented in the hierarchy of area divisions (see, for example, Myklestad & Birks 1993). Much more information on the relative strengths of different segments of border lines can be provided by 'Wombling' techniques, which measure rates of change in attribute values between adjacent grid cells (Womble 1951; Barbujani *et al.* 1989; Fortin 1994; Fortin & Drapeau 1995). These techniques for applying scores to grid-cell edges could be used to provide measures of the breadth of transition zones by changing the grain size of an analysis. For example, if strong border elements were identified at one spatial scale, then their frequencies could be compared within larger grid cells at a coarser spatial scale. Alternatively, a promising approach that does not impose discrete groups upon the data is ordination, although again, boundary information resides in the differences between scores for adjacent grid cells (on all sides), not directly within the individual grid-cell scores (cf. Orlóci & Orlóci 1990).

If the relative breadths of transition zones in two-dimensional spatial data are of interest, then it would be useful to be able to assign high scores to distinguish grid cells with transitional biota throughout the full breadth of the transition zones. These zones may be measured by restricting consideration to local neighbourhoods of grid cells and then asking where on a scale between spatial overlap and spatial replacement do the different patterns of species concordance lie (usage of 'overlap' for partial spatial concordance follows, for example, Pielou 1979; Rapoport 1982; Shmida & Wilson 1985; and 'replacement' for narrow spatial non-concordance follows, for example, Whittaker 1972; Rapoport 1982; Wilson & Shmida 1984; without necessarily implying any interaction between individuals, ecological equivalence, or other kind of relation). In principle, the spatial (i.e. geographical distribution) ranges of any two species, when reduced to presence–absence data at a particular spatial and temporal scale of investigation, must be somewhere on a continuum from: (i) completely overlapping, with (for grid data) no intersection of range limits (i.e. showing perfect 'nestedness' in the sense of Patterson & Atmar 1986, and no replacement); through (ii) partly overlapping, with intersecting range limits (i.e. showing some degree of partial nestedness and partial replacement); to (iii) completely non-overlapping, without intersection of range limits (i.e. showing no nestedness and complete replacement) (Pielou 1979; Rapoport 1982). In this paper I draw on previous measures of these three classes of patterns from studies of nested subsets of species, dissimilarity measures, and species/area-scaling (Whittaker's beta) measures.

2. MATERIALS AND METHODS

The spatial distributions of the 241 species of bumble bees recognized at present have been mapped provisionally as presence–absence data using a cylindrical equal-area projection of the world, divided into equal-area grid cells based on intervals of 10° longitude (each cell approximately 611000 km^2; Williams 1991, 1995*a*, *b*). To provide a basis for comparison with the results of turnover measures, a classification of the 247 occupied grid cells into biogeographic regions (figure 1) was obtained using the divisive polythetic clustering procedure TWINSPAN, which re-ordinates by reciprocal averaging before each division (see Hill 1979; Malloch 1988; Hengeveld 1990; Myklestad & Birks 1993). Classification procedures require stopping rules if groups of more than one area are to be obtained (Hengeveld 1990). Rules used in this coarse-scale analysis were: (i) making a maximum of five divisions; with (ii) a minimum divisible group size of 30 grid cells; and with (iii) no spatial contiguity constraints.

To examine spatial turnover of species within restricted parts of the map, comparisons were calculated within neighbourhoods of adjacent cells in the grid. This was done by considering each grid cell in turn along with its eight nearest neighbours (i.e. its first- and second-order neighbours, Smith 1994, using a moving-window on the grid, Johnston *et al.* 1992). The turnover measures were implemented using WORLDMAP software (Williams 1995*b*).

To assess the success of the neighbourhood turnover measures in discovering the same transition zones as those identified by the classification procedure TWINSPAN, randomization tests were made (Manly 1991). These tests assess whether scores in grid cells adjacent (as first- and second-order neighbours) to the regional border lines derived by TWINSPAN are higher than expected from random draws from among all scores for occupied grid cells. They are not intended as tests of the significance or of the generality of the resulting transition zones, which must be investigated using data randomizations and comparisons with other taxa (Pielou 1979).

3. NON-NESTEDNESS AS A MEASURE OF TURNOVER

Perfect spatial nestedness exists where the species present in any particular fauna are also present in all larger faunas, and where the species absent from any particular fauna are also absent from all smaller faunas (Cutler 1991). Viewed as an extreme form of species overlap, a pattern of nestedness may be seen as the antithesis of spatial replacement among species. Consequently, a measure of departures from nestedness (i.e. non-nestedness) might then be used to quantify the prevalence of spatial turnover in the broadest sense.

Consideration of colonization and extinction within archipelagos of islands (or habitat islands) led to attempts to quantify the degree of coincidence among species with different range sizes by using measures of spatial nestedness (Patterson & Atmar 1986; Cutler 1991; Simberloff & Martin 1991) or orderedness (Ryti

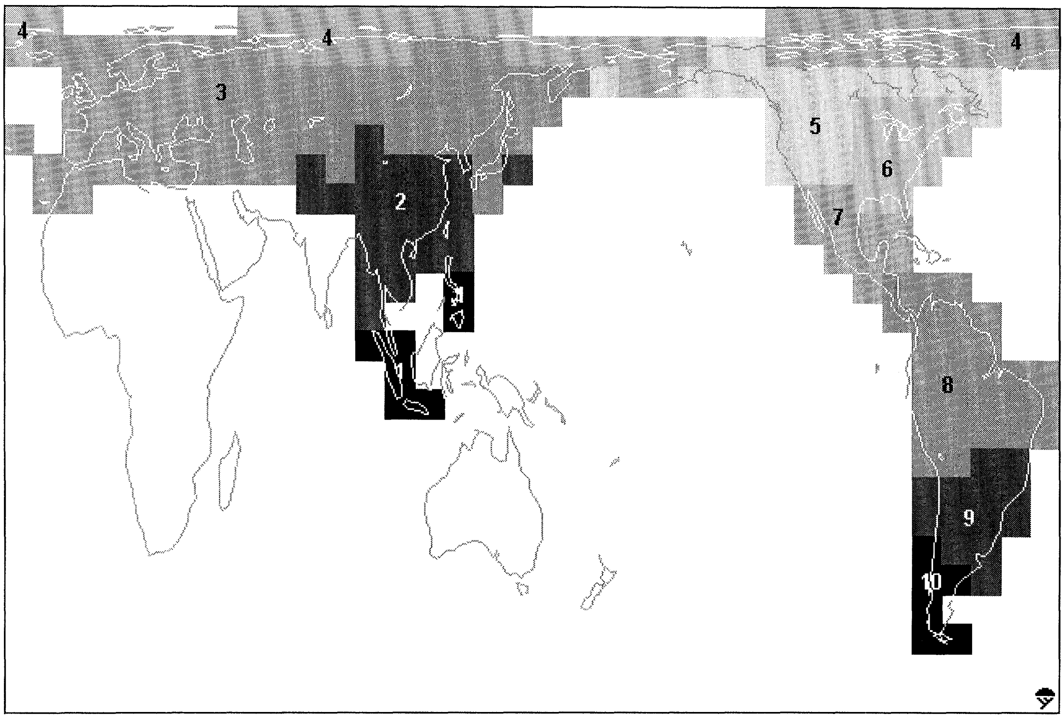

Figure 1. A total of ten principal biogeographic regions for bumble bees, shown as numbered contiguous areas of uniform grey. The classification was obtained using TWINSPAN (Hill 1979; Malloch 1988), from data for the 241 species on an equal-area (611000 km^2) grid (P. H. Williams, unpublished data). Numbered regions correspond approximately to biogeographic regions recognized for other taxa (Sclater 1858; Wallace 1876; Udvardy 1975): 1, southern Oriental region; 2, northern Oriental region; 3, Palaearctic region; 4, Arctic region; 5, western Nearctic region; 6, eastern Nearctic region; 7, southern Nearctic region; 8, northern Neotropical region; 9, central Neotropical region; 10, southern Neotropical region. The order of the region numbers follows the primary grid-cell ordination by TWINSPAN, although assignments of grey-scale intensities are arbitrary.

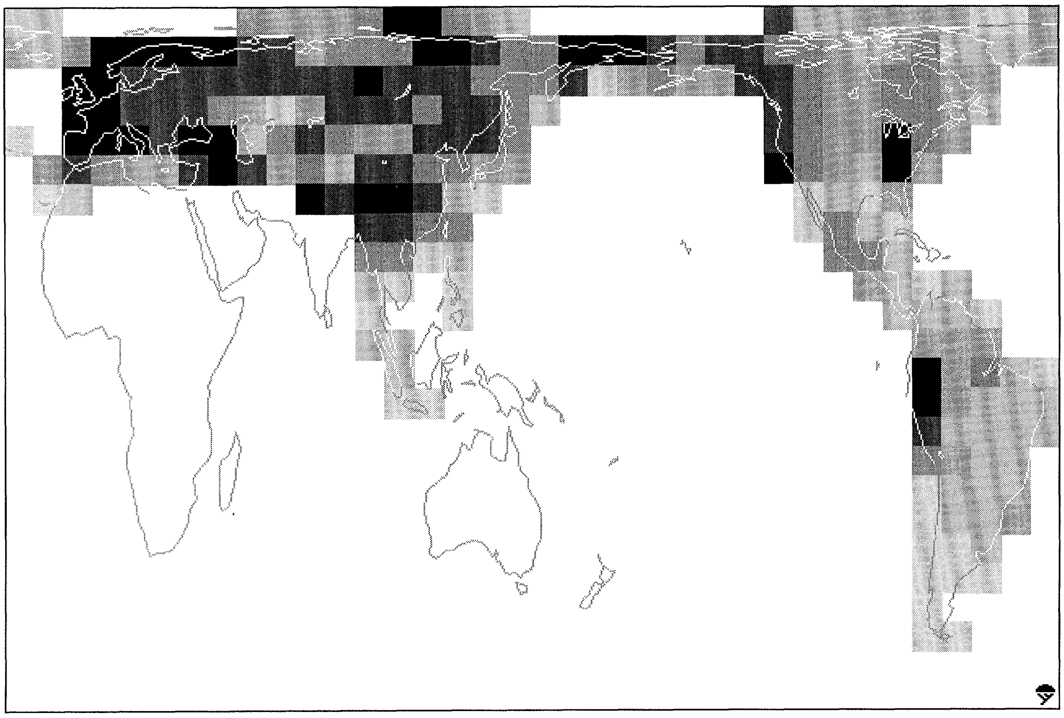

Figure 2. Centres combining high species richness with high species nestedness. Measured within neighbourhoods of nine grid cells (measure (2) $= 9as/(U+1)$, see text) and plotted using data for the 241 species of bumble bees on an equal-area (611000 km^2) grid (P. H. Williams, unpublished data). Scores are divided into six grey-scale classes of approximately equal size by numbers of grid cells.

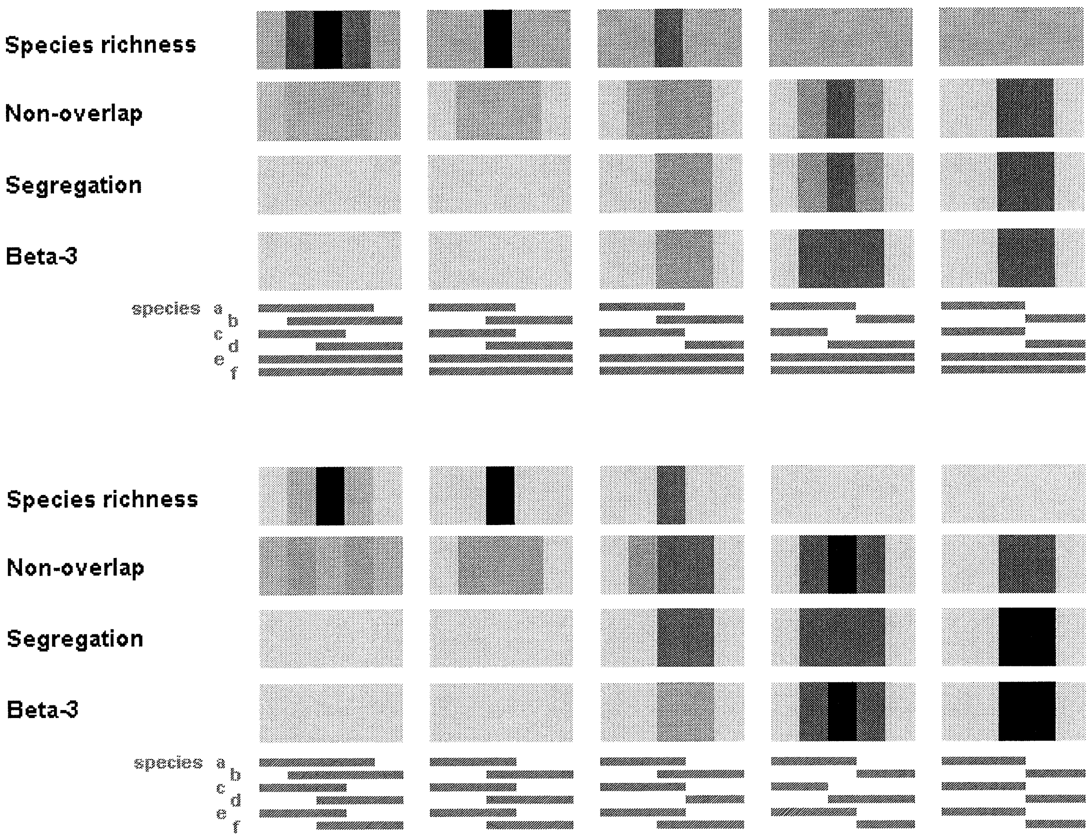

Figure 3. Turnover measures and species richness applied to simple test data for six species along transects crossing transition zones. Transition zones are weaker in the upper row, with only four out of six species contributing to turnover. Transition zones are narrower towards the right of both rows, with reduced spatial overlaps between species. Dissimilarity of 'non-overlap' measure (3) = $1-(\{\Sigma[c_{ij}/(c_i+c_j-c_{ij})]\}/[(s^2-s)/2])$; segregation measure (4) = $\{r+1\}/[\{s^2-s\}/2]$; and beta-3 measure (8) = $1-(a_{\max}/s)$, see text. Maximum scores are shown in black, other scores are divided into five grey-scale classes of approximately equal size by numbers of grid cells (as in figure 4). Although the particular numerical values differ, these frequency classes remain comparable among maps.

& Gilpin 1987). Cutler (1991) extended Patterson & Atmar's (1986) simple count of unexpected absences in a species-by-areas matrix to include the minimum number of both insertions (for 'holes' or unexpected absences) and deletions (for 'outliers' or unexpected presences) of species-in-area records that are required to convert the matrix to a pattern of perfect nestedness. These departures from nestedness are calculated for each species in turn, first by ranking the areas by species richness, and then by counting the minimum numbers of changes necessary to return the matrix to perfect nestedness, while allowing for any ties in species richness among areas (for worked examples, see Cutler 1991).

Numbers of departures from nestedness may be expressed as a proportion of the total size of the species-by-areas matrix for a neighbourhood:

$$\text{neighbourhood non-nestedness} = (U+1)/9s, \qquad (1)$$

where U is the minimum number of unexpected departures from nestedness in this neighbourhood and s is the total number of species in the neighbourhood of nine grid cells.

In addition, a measure to identify centres of highly nested species richness (giving high scores to grid cells that combine high species richness with high species nestedness) can be achieved by taking the inverse of measure (1) and by multiplying with the species richness, a, of the single core grid cell within each neighbourhood:

$$\text{neighbourhood nested richness} = 9as/(U+1). \qquad (2)$$

Measure (2) is plotted in figure 2 using data for bumble bees.

4. DISSIMILARITY AS A MEASURE OF TURNOVER

Similarity coefficients have been used before as direct measures of the spatial overlap between species (Rapoport 1982). They have also been used in some measures of spatial turnover at the scale of beta diversity (Whittaker 1960, 1972; Magurran 1988).

A simple measure of non-overlap among species may be formulated from the Jaccard (1912) similarity coefficient. For each grid cell in turn, the mean dissimilarity in distribution within the neighbourhood is calculated among all unique pairs of different species (for the triangular half-matrix, $i<j$):

$$\text{neighbourhood dissimilarity} = 1-(\{\Sigma[c_{ij}/(c_i+c_j-c_{ij})]\}/[(s^2-s)/2]), \qquad (3)$$

where c_i and c_j are the numbers of cells within a neighbourhood of up to nine grid cells occupied by species i and j respectively, c_{ij} is the number of cells shared by both, and s is the number of species in the neighbourhood (figures 3 and 4*a*).

Alternatively, complete spatial replacement among species can be measured, to exclude any overlap or partial replacement that may contribute to measure (3). This counts the proportion of pairwise comparisons among species for which there is no recorded overlap (the segregation index of Rapoport 1982):

$$\text{neighbourhood segregation} = (r+1)/[(s^2-s)/2], \quad (4)$$

where r is the number of unique pairwise (triangular half-matrix) species comparisons that show no overlap within a neighbourhood of up to nine grid cells, and s is the number of species in the neighbourhood (figure 3 and 4*b*).

5. SPECIES/AREA SCALING AS A MEASURE OF TURNOVER

Spatial turnover, when applied at an appropriate local scale, can be identical to the concept of beta diversity, whereas at broad spatial scales turnover has been associated with the concept of delta diversity (Whittaker 1972, 1977; Magurran 1988). Whittaker's (1960) original measure of beta diversity depends on the relation between species richness at different spatial scales:

$$\text{Whittaker } \beta = \gamma/\alpha, \quad (5)$$

where γ is the total number of species in a set of samples from a local community and α is the number of species in a single sample.

Wilson & Shmida (1984) reviewed measure (5) and five other measures of beta diversity and concluded that Whittaker's measure is the only one to meet all of their criteria when samples cannot be arranged along a single gradient. Harrison *et al.* (1992) modified Whittaker's measure and applied it at the larger spatial scale (in both grain size and survey extent) of 50 km × 50 km grid cells arranged along linear transects of Britain. They formulated a 'beta-1' measure to adjust for variations in transect extent:

$$\text{Harrison } et\ al. \text{ beta-1} = 100\ [(S/a_{\text{mean}})-1]/[C-1], \quad (6)$$

and a 'beta-2' measure to reduce the effect of trends in species richness across regions:

$$\text{Harrison } et\ al. \text{ beta-2} = 100\ [(S/a_{\text{max}})-1]/[C-1], \quad (7)$$

where S is the number of species in a region, a_{mean} is the mean number of species per grid cell, a_{max} is the maximum number of species per grid cell, and C is the number of grid cells (both measures were expressed as percentages).

In this paper, a modified measure of spatial turnover is applied to neighbourhoods of grid cells within a two-dimensional grid. The reduced sensitivity to trends in grid-cell richness across regions that was added in measure (7) is still needed to prevent the measure responding strongly to simple trends in species richness without replacement, for example towards the edges of a group's distribution. On the other hand, the adjustment for regions of different sizes, in this case for different numbers of occupied grid cells within a neighbourhood, that was added in measure (6) is not desirable (the same is true for measures 1, 2 and 4). This is because a measure relative to occupancy would over-value the contribution of small absolute amounts of turnover in partly occupied neighbourhoods (e.g. at continental margins):

$$\text{neighbourhood beta-3} = 1-(a_{\text{max}}/s), \quad (8)$$

where s is the number of species in a neighbourhood of up to nine grid cells, and a_{max} is the maximum number of species per grid cell in the neighbourhood (figure 3 and 4*c*).

6. RESULTS AND DISCUSSION

Bumble bees are unusual (though by no means unique) in that they are associated particularly with cool and strongly seasonal environments (Williams 1991, 1995*a*). They are also absent from Africa south of the Sahara, from lowland India, from Australia and from Oceania. In spite of this, a regional classification of bumble bee faunas by TWINSPAN (figure 1) shows strong similarities at the broadest scales to the previous regional classifications based on many other animal and plant taxa (Sclater 1858; Wallace 1876; Udvardy 1975), for example, in distinguishing Palaearctic, Oriental, western Nearctic, eastern Nearctic, southern Nearctic, northern Neotropical, central Neotropical and southern Neotropical faunas. The largest difference is in the recognition of a nearly circumpolar Arctic fauna for bumble bees. Inevitably though, regions defined by classification techniques are dependent to some extent on the particular stopping rules applied, so one would expect other rules to result in other regional border lines. For example, setting the minimum divisible group to 30 cells has prevented the southern Malay Peninsula, Sumatra and Java from being classified separately from the southern Philippines, a grouping of bumble-bee faunas which is very unlikely to reflect an exclusively shared historical relation (Starr 1989). An important question is then: how comparable are the different parts of transition zones between regions?

Spatial turnover measures (measures 3, 4 and 8), with the exception of non–nestedness (measure 1), did succeed in recovering a similar pattern of the principal biogeographic regions for bumble bees to the TWINSPAN classification, as shown by the significantly higher turnover scores along the border lines of the biogeographic regions (randomisation test, table 1). Of course it should be clear from the description of the methods that the neighbourhood turnover approach is not constrained to ensure that grid cells with high scores are always arranged in lines, or that these high scores should necessarily completely encircle regions. The failure of the measure of non-nestedness (measure 1) to recover the TWINSPAN pattern results from its inherently greater sensitivity to broad spatial overlap within neighbourhoods. Such broadly overlapping species are less likely to be informative for the discrimination of biogeographic regions. In contrast,

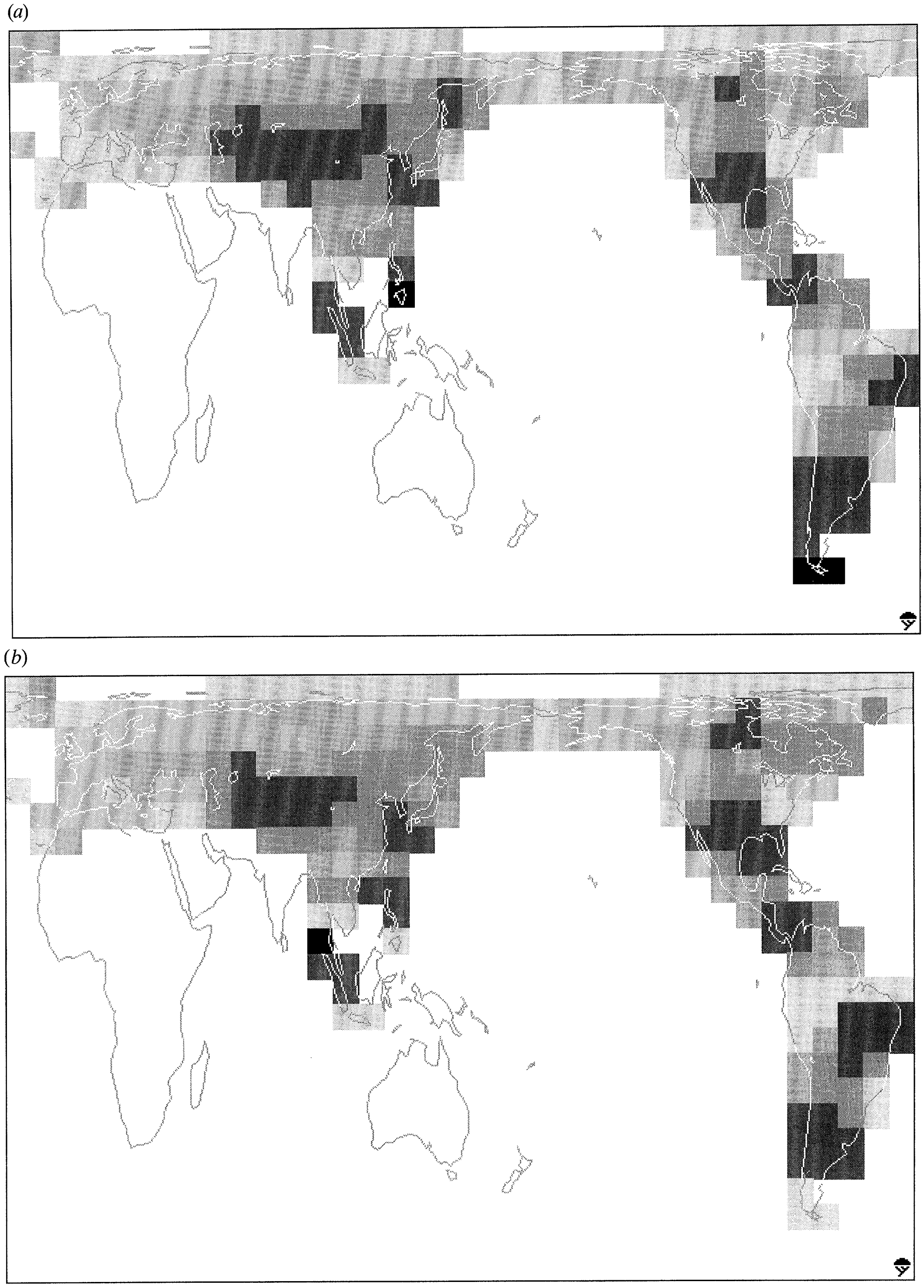

Figure 4 (*a*, *b*). For legend see facing page.

high scores for the other turnover measures (3, 4, 8) reflect the stronger contribution of patterns of complete species replacement to the regional border lines recognized by TWINSPAN. When these turnover scores are mapped (figure 4), the general association of the high scores (as dark grey cells) with the biogeographic border lines from figure 1 can be seen (perhaps particularly clearly for beta-3 in figure 4*c*). The principal exception is that the turnover scores do not support strong transition zones to the Arctic region (cf. figure 1: region 4). The fauna of this region is relatively poor (Williams 1995*a*: figure 1), and consists largely of a subset of the species found further south. However, about one fifth (19 %) of the Arctic fauna is contributed by the characteristically high-Arctic species of the subgenus *Alpinobombus* (Skorikov 1937), which provide the only two positive indicator species (*B. hyperboreus* and *B. polaris*) used by TWINSPAN to define the Arctic region.

Common patterns of variation in the intensity of high scores for species turnover (dark grey areas in figure 4) along the lengths of the biogeographic border

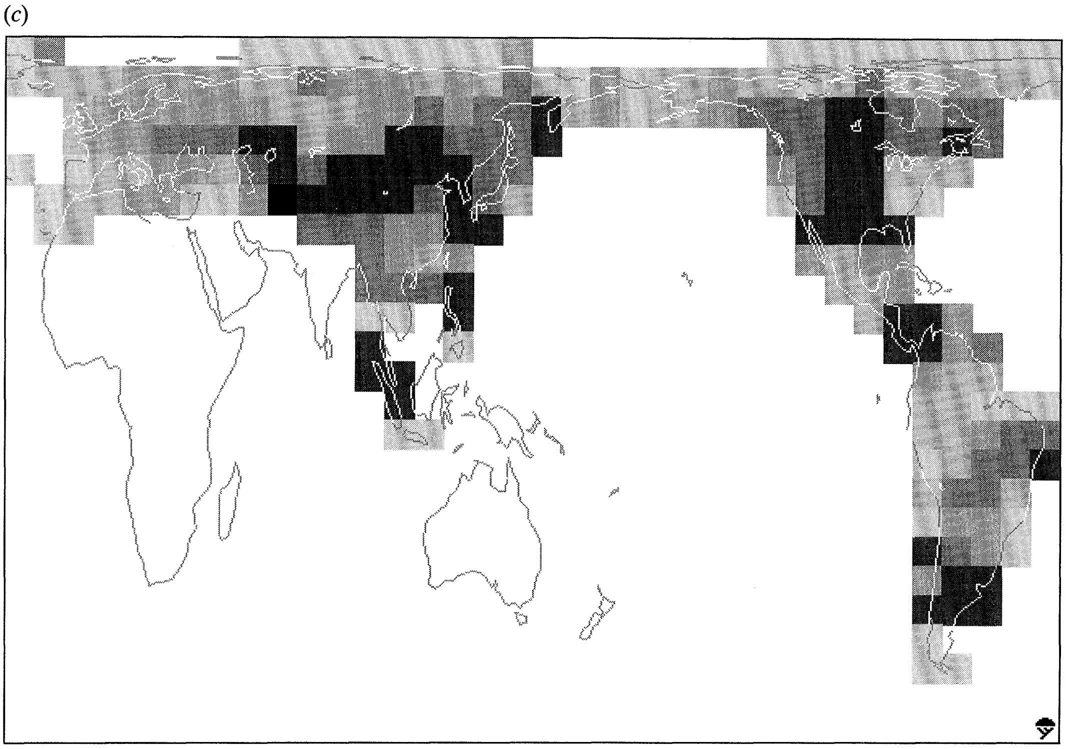

Figure 4. Zones of high species turnover. (*a*) Measured as species dissimilarity within neighbourhoods of nine grid cells (measure (3) $= 1-(\{\Sigma[c_{ij}/(c_i+c_j-c_{ij})]\}/[(s^2-s)/2])$, see text). (*b*) Measured as complete species segregation within neighbourhoods of nine grid cells (measure (4) $= \{r+1\}/[\{s^2-s\}/2]$, see text). (*c*) Measured using the beta-3 formula within neighbourhoods of nine grid cells (measure (8) $= 1-\{a_{\max}/s\}$, see text). Maps are plotted using data for the 241 species of bumble bees on an equal-area (611000 km^2) grid (P. H. Williams, unpublished data). Grey-scale for score classes as in figure 3.

Table 1. *Association of species turnover scores with species richness, centres of nested richness and biogeographic border lines*

(To test for association of high species turnover scores with biogeographic border lines, the observed mean score for the 145 grid cells situated as neighbours to the internal borders from figure 1 is compared with the distribution of mean scores from 10000 random draws of 145 cells without replacement from among the 247 occupied cells. Note: as with most comparisons between values for areas on transects or maps, the probabilities of these associations may be exaggerated by spatial autocorrelation.)

turnover measures	species richness (Williams 1995*a*: figure 1) [Spearman rank correlation rho (single-tailed *p*)]	centres of nested richness by measure (2) (figure 2) [Spearman rank correlation rho (single-tailed *p*)]	biogeographic border lines by TWINSPAN (figure 1) [mean observed score/mean expected score by random draws (single-tailed *p*)]
non-nestedness measure (1)	0.45 (< 0.0005)	−0.08 (> 0.05)	1.04 (> 0.05)
dissimilarity measure (3) (figure 4*a*)	0.05 (> 0.05)	−0.35 (< 0.0005)	1.05 (< 0.0001)
segregation measure (4) (figure 4*b*)	0.09 (> 0.05)	−0.27 (< 0.0005)	1.31 (< 0.0001)
beta-3 measure (8) (figure 4*c*)	0.29 (< 0.0005)	−0.11 (< 0.05	1.20 (< 0.0001)
centres of nested richness measure (2) (figure 2)	0.82 (< 0.0005)	1	0.88 (< 0.01)

lines (see figure 1) show the varying strengths of the transition zones for bumble bees, in the sense of the varying proportions of species involved in replacement. This is demonstrated in figure 3, where the lower group of examples, in which all six species are involved in replacement, generate higher turnover scores than the upper group, in which only four out of six species show replacement. One of the more consistent patterns among the turnover measures on the maps (figure 4) is the decreasing strength of the transition zone between the northern and central Neotropical regions (cf. figure 1: regions 8–9) from east to west. In the east, this reflects strong latitudinal variation in the composition of the faunas of low-to-mid altitudes (species of the subgenus *Fervidobombus*). In the west, these latitudinal patterns are complicated and obscured by stronger altitudinal effects within the richer, montane fauna of the Andes (adding to *Fervidobombus* the South American species of the *sibiricus*-group of subgenera: *Robustobombus*, *Funebribombus*, *Brachycephalibombus*, *Rubicundobombus*, *Coccineobombus* and *Dasybombus* in the broad sense, Williams *et al.* 1993; Williams 1995*a*).

Differences between the maps in the patterns of high turnover scores along the biogeographic border lines are expected (i.e. between dark grey areas in figure 4), because of the differing sensitivities of the measures to broader transition zones with part species overlap (varying breadth of transition zones may not be strongly apparent within each map in part because the grid cells are so large). Figure 3 employs the same grey-scale as the maps and demonstrates for the simple test data that the dissimilarity measure (3) is most responsive to partial spatial overlap among species, whereas the segregation measure (4) is least responsive. For example, in figure 4*a*, *b* differences between the patterns of high scores for these measures are apparent along the transition zone between the Palaearctic and Oriental regions of the Old World (figure 1: regions 2–3), particularly as lower scores in the east for the segregation measure (figure 4*b*). This is interpreted as showing changes in composition of bumble bee faunas that are much more abrupt in the west (around Kashmir, as reported by Williams 1991) than in the east (in the vicinity of Beijing, as reported by Panfilov 1957). The existence of narrower boundaries in the west is presumably related to the conjunction of three particularly high and extensive mountain systems (broadly, the Hindu Kush, Pamir–Tien Shan and Himalaya–Tibet), which not only contribute (as barriers to atmospheric circulation) to steepened macro-climatic gradients between these regions (Chang 1981), but also provide barriers of habitat unsuitable to the spread of bumble bees, both as many mountain ridges with snow and as deep arid valleys (Williams 1991). Figure 3 also shows that the beta-3 and segregation measures may give very similar patterns of scores, although beta-3 is sensitive to turnover with some narrow spatial overlap among species. This may explain some of the differences between patterns of scores for these measures in the New World (figure 4*b*, *c*). For example, the beta-3 measure gives consistently high scores in the transition zone between the bumble bee faunas of the eastern and western Nearctic regions in the midwest of the United States (figure 1: regions 5–6), whereas the scores for the segregation measure, although high in the southern states, decline in the northern states. Thus the transition zone between these bumble bee faunas appears to be more abrupt in the southern United States (where suitable mesic habitat is interrupted broadly by semi-arid areas), but forms a broader transition in the more northerly United States (where suitable habitat is more continuous).

Negative correlations between scores for nested richness (measure 2) and scores for dissimilarity, segregation and beta-3 (table 1) show that for bumble bees at this coarse scale, transition zones tend to circumscribe centres that combine high species richness with high species nestedness (in contrast, the relation of these turnover measures with simple species richness is not consistent, table 1). Not surprisingly then, for these data, centres of nested richness tend to occur away from the border lines of the biogeographic regions (randomisation test, table 1). In the Old World (figure 2), strong centres of bumble-bee nested richness occur in western Europe, around Armenia, and in Siberia within the Palaearctic region, and in the Himalaya and southern China within the Oriental region. In the New World, strong centres of bumble-bee nested richness occur in California within the western Nearctic, in the Appalachians of the eastern Nearctic, and in the Andes of the northern Neotropical region. The high scores in the eastern Russian Arctic reflect a greater contribution from nestedness than from richness (cf. Williams 1995*a*: figure 1).

The measures used in this paper are applicable at any spatial scale, just as area-classification techniques are essentially scale-independent (Myklestad & Birks 1993). In contrast, the results are likely to be strongly dependent on spatial scale, with regard to both survey extent (worldwide, continentwide etc.) and grain size (grid-cell size). Measures of species turnover are expected to be particularly sensitive to grain size (Rapoport 1982; Gosz 1993; Gaston 1994) because of species-area effects. The bumble bee data used as an example in figure 4 were deliberately compiled at a broad and coarse-grained spatial scale for the purpose of investigating regional species pools. At this scale, it must be remembered that any overlap (partial concordance) of records in a grid cell does not necessarily imply local co-occurrence among species. Perhaps particularly at finer grain sizes, if species have very patchy, fragmented or mosaic distributions, then transition zones evident at coarser spatial scales are likely to become obscured by this more local turnover. Increasing the number of grid cells in each neighbourhood may then be appropriate if the transition zones of interest are not very close together. However, larger neighbourhoods will tend to reduce the proportion of species showing perfect neighbourhood nestedness or perfect replacement, because it will increase the likelihood of discovering partial overlap.

The beta-3 measure may be particularly promising for future study. Like the segregation measure, it shows close association of high scores with the border lines recognized by TWINSPAN (table 1). But unlike the segregation measure, beta-3 can be sensitive to turnover despite partly overlapping distributions within a neighbourhood, which may be useful with larger neighbourhoods. Beta-3 is also much faster to calculate than any of the other measures. However, a potential weakness of beta-3 is that it is more strongly influenced by the precision of the single highest estimate for grid-cell richness within each neighbourhood.

Measures of spatial turnover based on dissimilarity and species/area scaling offer another heuristic approach to recognizing the location and nature of transition zones that has potential for complementing existing techniques, at least at broad spatial scales. In principle, these turnover measures should be applicable at any spatial scale, from local communities to global regions. At the global scale, it still remains to be seen how far the resulting patterns may be generalized among taxa, largely because comprehensive species data are available for so few higher taxa of any size.

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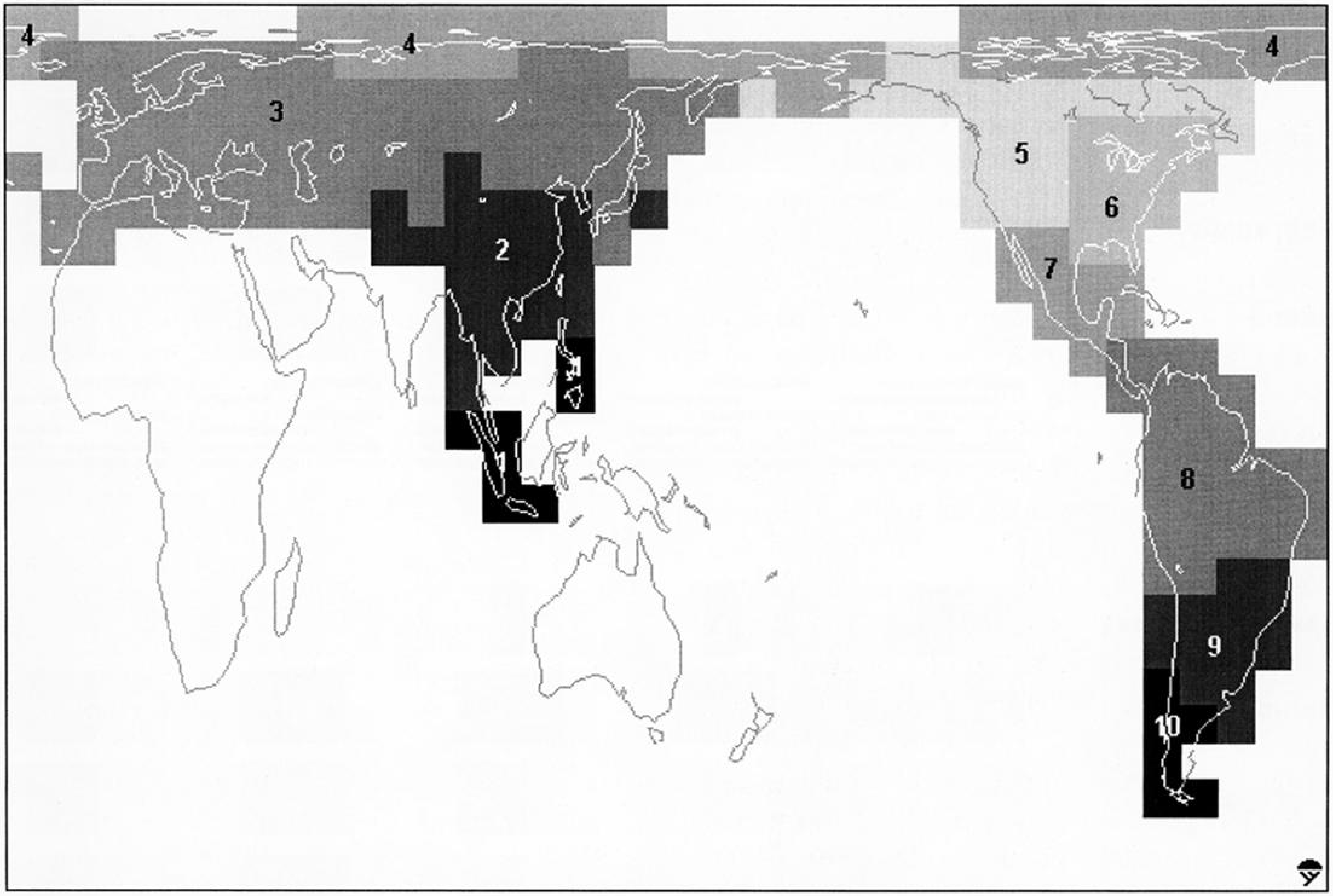

Figure 1. A total of ten principal biogeographic regions for bumble bees, shown as numbered contiguous areas of uniform grey. The classification was obtained using TWINSPAN (Hill 1979; Malloch 1988), from data for the 241 species on an equal-area (611 000 km²) grid (P. H. Williams, unpublished data). Numbered regions correspond approximately to biogeographic regions recognized for other taxa (Sclater 1858; Wallace 1876; Udvardy 1975): 1, southern Oriental region; 2, northern Oriental region; 3, Palaearctic region; 4, Arctic region; 5, western Nearctic region; 6, eastern Nearctic region; 7, southern Nearctic region; 8, northern Neotropical region; 9, central Neotropical region; 10, southern Neotropical region. The order of the region numbers follows the primary grid-cell ordination by TWINSPAN, although assignments of grey-scale intensities are arbitrary.

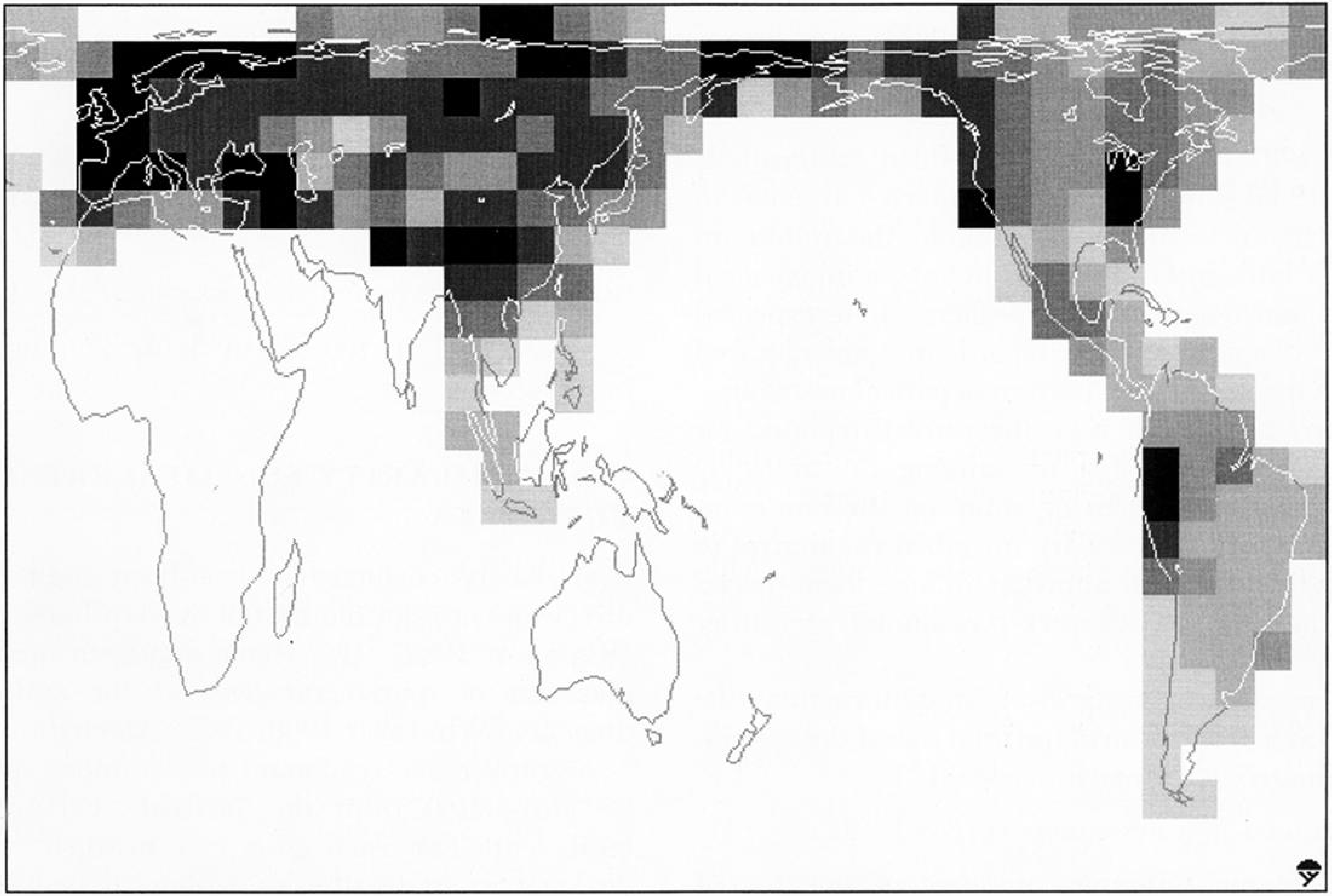

Figure 2. Centres combining high species richness with high species nestedness. Measured within neighbourhoods of nine grid cells (measure (2) = $9as/(U+1)$, see text) and plotted using data for the 241 species of bumble bees on an equal-area (611 000 km^2) grid (P. H. Williams, unpublished data). Scores are divided into six grey-scale classes of approximately equal size by numbers of grid cells.

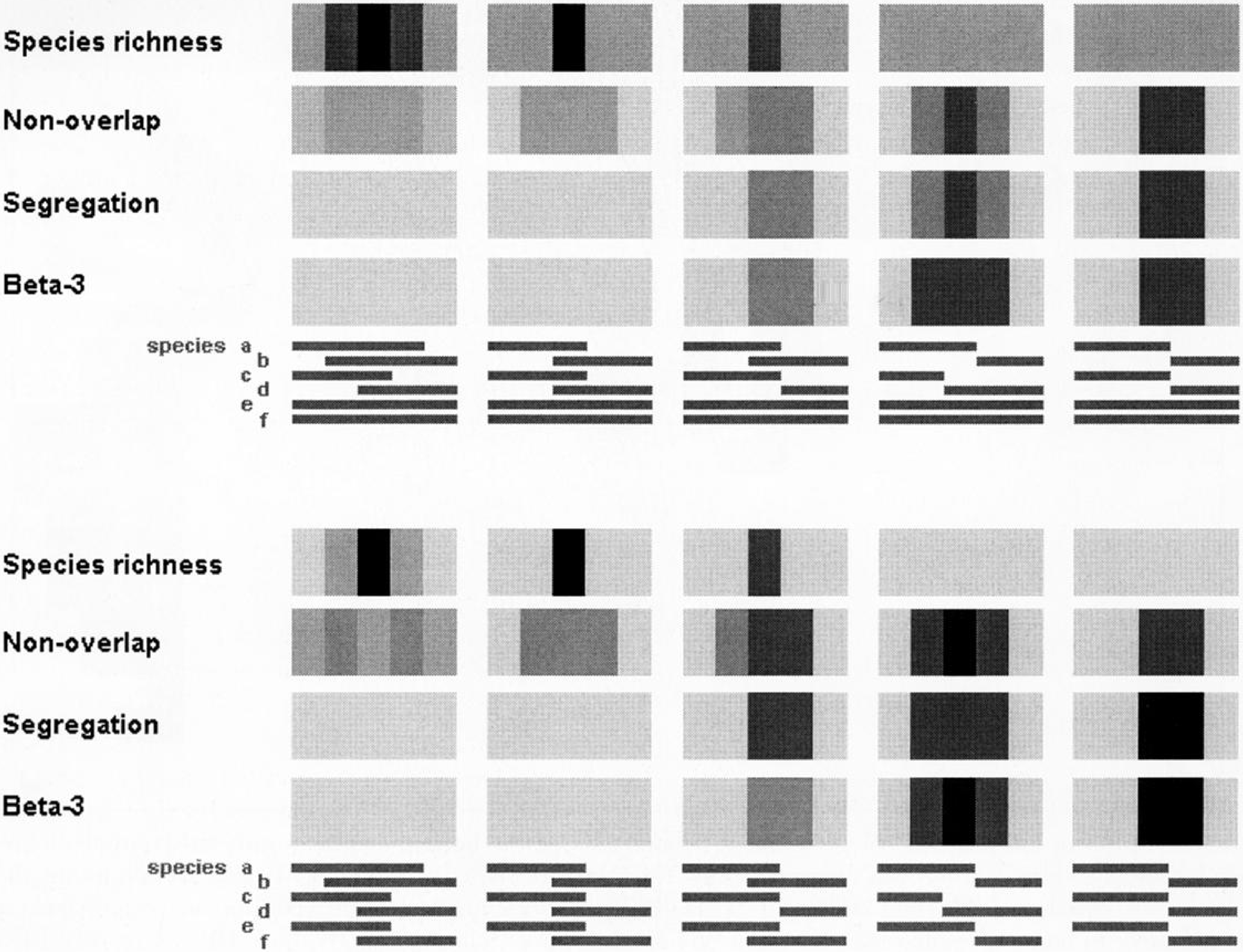

Figure 3. Turnover measures and species richness applied to simple test data for six species along transects crossing transition zones. Transition zones are weaker in the upper row, with only four out of six species contributing to turnover. Transition zones are narrower towards the right of both rows, with reduced spatial overlaps between species. Dissimilarity of 'non-overlap' measure (3) = $1-(\{\Sigma[c_{ij}/(c_i+c_j-c_{ij})]\}/[(s^2-s)/2])$; segregation measure (4) = $\{r+1\}/[\{s^2-s\}/2]$; and beta-3 measure (8) = $1-(a_{\max}/s)$, see text. Maximum scores are shown in black, other scores are divided into five grey-scale classes of approximately equal size by numbers of grid cells (as in figure 4). Although the particular numerical values differ, these frequency classes remain comparable among maps.

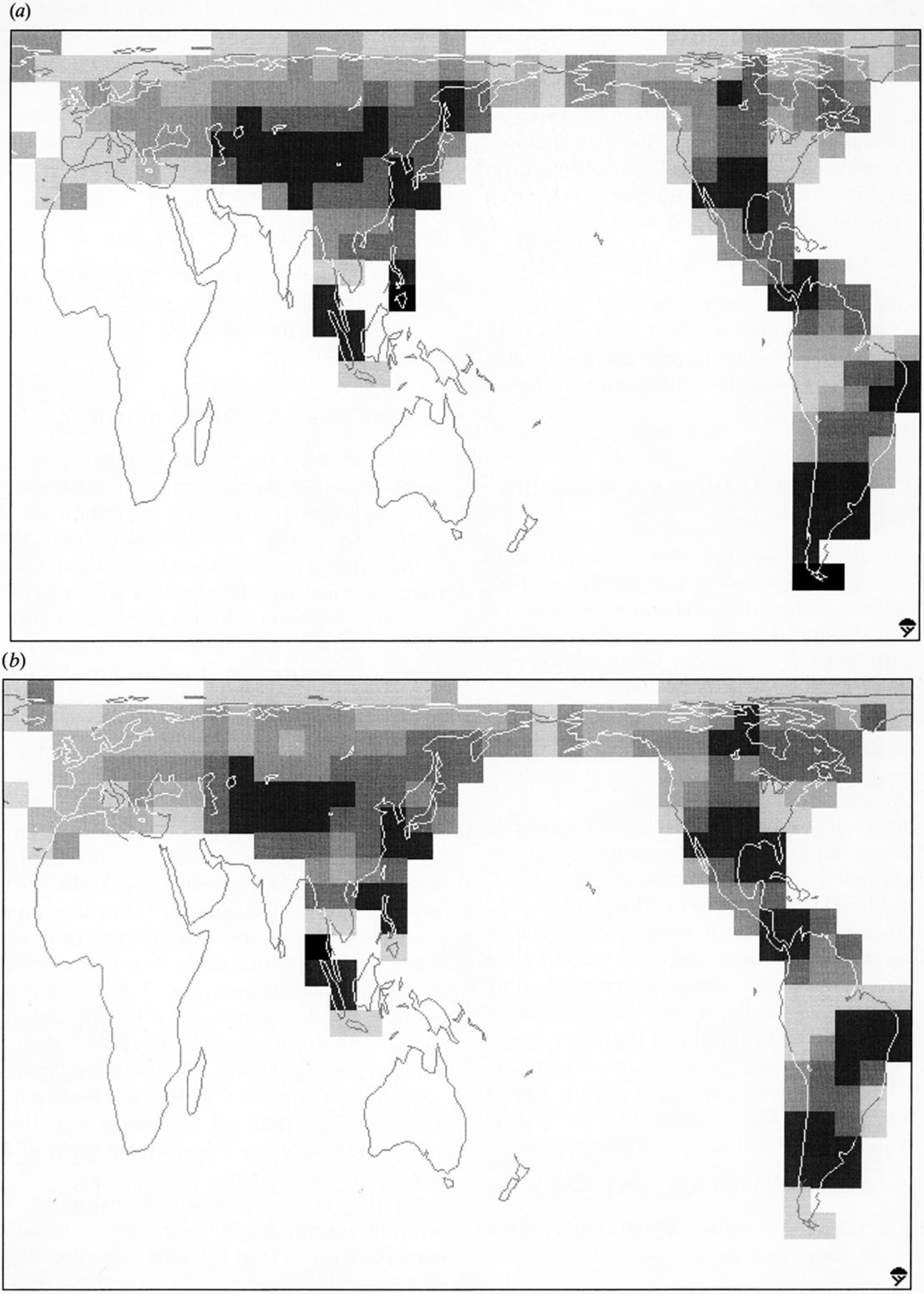

Figure 4 (*a*, *b*). For legend see facing page.

(*c*)

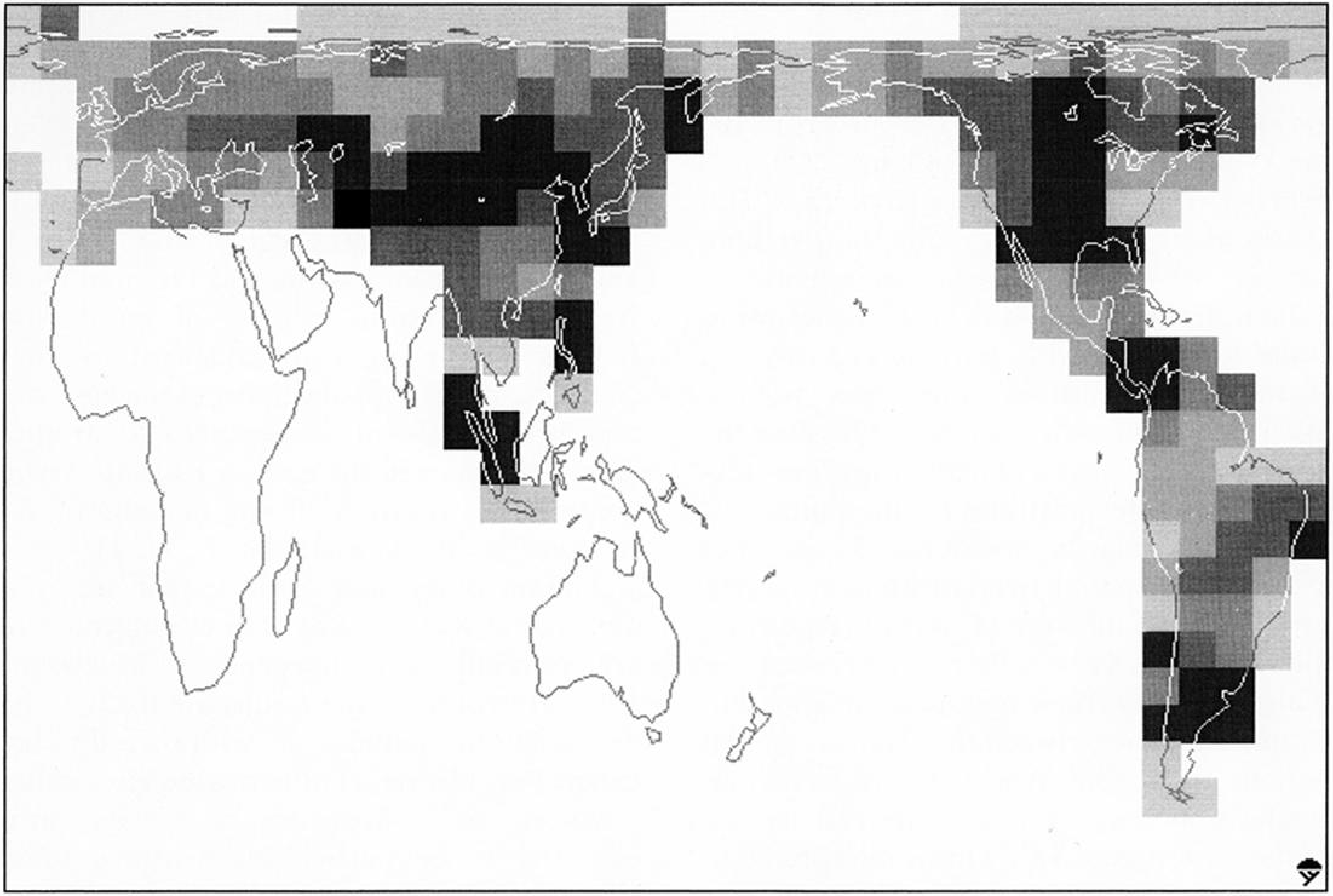

Figure 4. Zones of high species turnover. (*a*) Measured as species dissimilarity within neighbourhoods of nine grid cells (measure (3) $= 1-(\{\Sigma[c_{ij}/(c_i+c_j-c_{ij})]\}/[(s^2-s)/2])$, see text). (*b*) Measured as complete species segregation within neighbourhoods of nine grid cells (measure (4) $= \{r+1\}/[\{s^2-s\}/2]$, see text). (*c*) Measured using the beta-3 formula within neighbourhoods of nine grid cells (measure (8) $= 1-\{a_{\max}/s\}$, see text). Maps are plotted using data for the 241 species of bumble bees on an equal-area (611000 km²) grid (P. H. Williams, unpublished data). Grey-scale for score classes as in figure 3.