

Measuring beta diversity for presence–absence data

PATRICIA KOLEFF*†, KEVIN J. GASTON* and JACK J. LENNON‡

*Biodiversity and Macroecology Group, Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK; and †The Macaulay Institute, Craigiebuckler, Aberdeen AB15 8QH, UK

Summary

1. Little consensus has been reached as to general features of spatial variation in beta diversity, a fundamental component of species diversity. This could reflect a genuine lack of simple gradients in beta diversity, or a lack of agreement as to just what constitutes beta diversity. Unfortunately, a large number of approaches have been applied to the investigation of variation in beta diversity, which potentially makes comparisons of the findings difficult.
2. We review 24 measures of beta diversity for presence/absence data (the most frequent form of data to which such measures are applied) that have been employed in the literature, express many of them for the first time in common terms, and compare some of their basic properties.
3. Four groups of measures are distinguished, with a fundamental distinction arising between ‘broad sense’ measures incorporating differences in composition attributable to species richness gradients, and ‘narrow sense’ measures that focus on compositional differences independent of such gradients. On a number of occasions on which the former have been employed in the literature the latter may have been more appropriate, and there are many situations in which consideration of both kinds of measures would be valuable.
4. We particularly recommend (i) considering beta diversity measures in terms of matching/mismatching components (usually denoted a , b and c) and thereby identifying the contribution of different sources of variation in species composition, and (ii) the use of ternary plots to express the relationship between the values of these measures and of the components, and as a way of understanding patterns in beta diversity.

Key-words: beta diversity, biodiversity, presence–absence, similarity indices, spatial turnover.

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Introduction

Ecologists have long distinguished between different components of species diversity. Traditionally, three are recognized, alpha or local diversity (α), beta diversity or differentiation (β) and gamma or regional diversity (γ). Beta diversity, the spatial turnover or change in the identities of species, is a measure of the difference in species composition either between two or more

local assemblages or between local and regional assemblages. For a given level of regional species richness, as beta diversity increases, individual localities differ more markedly from one another and sample a smaller proportion of the species occurring in the region. As has long been recognized, it thus captures a fundamental facet of the spatial pattern of biodiversity (Whittaker 1960, 1972; Cody 1975; Wilson & Shmida 1984; Shmida & Wilson 1985; Gaston & Williams 1996). None the less, it has received surprisingly limited attention, particularly when contrasted with the vast number of studies of local or alpha diversity; arguably this is increasingly true also when contrasted with the attention that is being paid to regional or gamma diversity in the context of broad-scale patterns of variation in species richness and their determinants (for reviews see Brown 1995; Gaston & Blackburn 2000; Gaston 2000; Blackburn & Gaston 2003).

Correspondence: Kevin J. Gaston, Biodiversity and Macroecology Group, Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK. Tel.: 0114 2220030; Fax: 0114 2220002; E-mail: k.j.gaston@sheffield.ac.uk

†Present address: CONABIO, Avenue Liga Periférico, Insurgentes Sur 4903, Col. Parques del Pedregal, Delegación Tlalpan, 01410 México, DF, México.

Notwithstanding, several generalizations have been made about the form that spatial patterns in beta diversity are likely to take. Foremost among these is the assertion that spatial turnover in species identities increases towards lower latitudes, providing a proximate mechanism for the high levels of tropical species richness (Gaston & Williams 1996; Mourelle & Ezcurra 1997; Brown & Lomolino 1998). A number of recent studies have sought empirically to test such generalizations (Harrison, Ross & Lawton 1992; Willig & Sandlin 1992; Blackburn & Gaston 1996; Mourelle & Ezcurra 1997; Clarke & Lidgard 2000). Their findings have been inconsistent, suggesting that any patterns may be strongly contingent on taxon or geographical region. However, comparisons between the results of different studies may be hindered severely by the variety of measures that have been used to quantify beta diversity and by the variety of ways in which these measures have been applied. These problems are seldom acknowledged and the results of different analyses are in judiciously, and not infrequently, treated as if they were strictly comparable (Gaston & Williams 1996).

Since Whittaker's (1960, 1972) original suggestion that beta diversity should be measured as the proportion by which the species richness of a region exceeds the average richness of a single locality within that region, numerous measures have been proposed that constitute variations on this theme (Cody 1975; Routledge 1977, 1984; Wilson & Shmida 1984; Magurran 1988; Harrison *et al.* 1992; Williams 1996a; Harte & Kinzig 1997; Mourelle & Ezcurra 1997). Indeed, arguably, almost for each new application of the concept of beta diversity a fresh measure has been derived, with studies employing measures of beta diversity to address such issues as the changes in species composition along spatial or environmental gradients (MacArthur 1965; Whittaker 1960, 1972; Cody 1975; Routledge 1977; Wilson & Shmida 1984; Harrison *et al.* 1992; Blackburn & Gaston 1996; Mourelle & Ezcurra 1997; Willig & Gannon 1997) and between patches of similar habitats (Whittaker 1977; Harrison 1997); the degree of association or similarity of sites or samples (Magurran 1988; Price *et al.* 1999); and the identification of biogeographical boundaries or transition-zone patterns and their implications for conservation planning (Poynton & Boycott 1996; Williams 1996a; Ruggiero, Lawton & Blackburn 1998; Williams, de Klerk & Crowe 1999; Gaston *et al.* 2001). Efforts have been made to compile and compare selected measures of beta diversity (see Routledge 1984; Wilson & Shmida 1984; Magurran 1988; Williams 1996a; Krebs 1999; Southwood & Henderson 2000). Some measures are clearly closely correlated, at least under some conditions, while others give wildly different patterns of results for the same data sets (Wilson & Shmida 1984; Blackburn & Gaston 1996; Williams 1996a; Williams *et al.* 1999; Clarke & Lidgard 2000). In general, however, the reasons for using, or preferring, any particular measure rather than another remain unclear. Around half of the studies

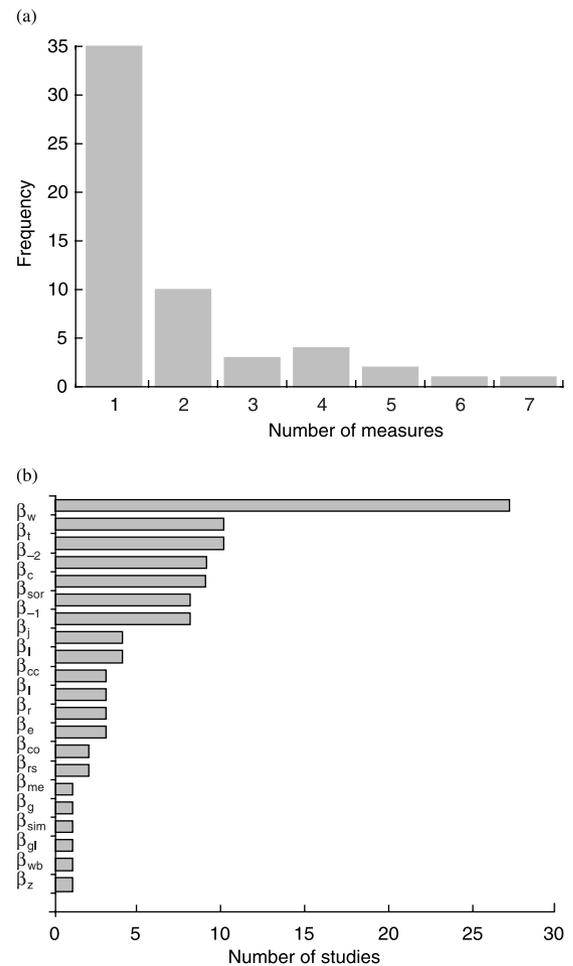


Fig. 1. (a) The number of studies employing different numbers of measures of beta diversity, and (b) the number of times that each beta diversity measure has been used, based on 60 publications that have employed at least one of the measures in Table 1.

of beta diversity have used more than one measure (Fig. 1a), although Whittaker's original measure (β_w) has been the most frequently employed (Fig. 1b).

In this study, we collate the 24 published measures of beta diversity based on presence/absence data of which we are aware (the vast majority of explicit studies of beta diversity have focused on presence/absence data). These are then, often for the first time, expressed in common terms, and some of their basic properties are compared. The main issues addressed are what beta diversity measures actually measure, how measures differ, and the importance of the differences. This exercise reveals that existing measures divide into a few basic groups, each of which captures a different facet of spatial turnover in the identities of species. We do not enter into debate as to the relative merits of multiplicative and additive approaches to the relations between alpha, beta and gamma diversity measures, while acknowledging that recent discussion of the latter addresses a potentially exciting avenue of investigation (Lande 1996; Loreau 2000; Veech *et al.* 2002).

Table 1. Beta diversity measures for presence/absence data, identified by subscripted 'β's, and given in terms of their original formulation (described in common algebraic notation) and re-expressed in terms of matching components (see Fig. 2 for the definition of *a*, *b*, and *c*) for a pair of quadrats. Numbers in bold indicate those measures whose performance was examined

	Original formulation	Measure re-expressed	Source
1	$\beta_w \frac{S}{\bar{\alpha}} \text{ or } \frac{S}{\bar{\alpha}} - 1$	$\frac{a+b+c}{(2a+b+c)/2} \text{ or } \frac{a+b+c}{(2a+b+c)/2} - 1$	Whittaker (1960), see also Magurran (1988), Southwood & Henderson (2000)
2	$\beta_{-1} \left[\frac{S}{\bar{\alpha}} - 1 \right] / (N-1)$	$\frac{a+b+c}{(2a+b+c)/2} - 1$	Harrison <i>et al.</i> (1992)
3	$\beta_c \frac{g(H)+l(H)}{2}$	$\frac{b+c}{2}$	Cody (1975)
4	$\beta_{wb} (a+b) + (a+c) - 2a$	$b+c$	Weiherr & Boylen (1994)
5	$\beta_r \frac{S^2}{2r+S} \text{ or } \frac{S^2}{2r+S} - 1$	$\frac{(a+b+c)^2}{(a+b+c)^2 - 2bc} \text{ or } \frac{(a+b+c)^2}{(a+b+c)^2 - 2bc} - 1$	Routledge (1977), see also Magurran (1988), Southwood & Henderson (2000)
6	$\beta_t \log(T) - \left(\frac{1}{T} \sum_i e_i \log(e_i) \right) - \left(\frac{1}{T} \sum_j \alpha_j \log(\alpha_j) \right)$	$\log(2a+b+c) - \left(\frac{1}{2a+b+c} 2a \log 2 \right) - \left(\frac{1}{2a+b+c} ((a+b) \log(a+b) + (a+c) \log(a+c)) \right)$	Routledge (1977), Wilson & Shmida (1984)
7	β_e	$\exp(\beta_t) - 1$	Routledge (1977)
8	$\beta_t \frac{g(H)+l(H)}{2\bar{\alpha}}$	$\frac{b+c}{2a+b+c}$	Wilson & Shmida (1984)
9	$\beta_{mc} \frac{g(H)+l(H)}{2\bar{\alpha}(N-1)}$	$\frac{b+c}{2a+b+c}$	Mourelle & Ezcurra (1997)
10	$\beta_j \frac{a}{\alpha_1 + \alpha_2 - a}$	$\frac{a}{a+b+c}$	Jaccard (1912), see also Magurran (1988), Southwood & Henderson (2000)
11	$\beta_{sor} \frac{2a}{\alpha_1 + \alpha_2}$	$\frac{2a}{2a+b+c}$	Sørensen (1948) based on Dice (1945); see also Whittaker (1975), Magurran (1988), Southwood & Henderson (2000)
12	$\beta_m (\alpha_1 + \alpha_2)(1 - \beta_j)$	$(2a+b+c) \left(1 - \frac{a}{a+b+c} \right)$	Magurran (1988)
13	$\beta_{-2} \left[\frac{S}{\bar{\alpha}_{\max}} - 1 \right] / (N-1)$	$\frac{\min(b,c)}{\max(b,c) + a}$	Harrison <i>et al.</i> (1992) ¹
14	$\beta_{co} 1 - \frac{C(T_1+T_2)}{2T_1T_2}$	$1 - \frac{a(2a+b+c)}{2(a+b)(a+c)}$	Cody (1993)
15	$\beta_{cc} \frac{\alpha_1 + \alpha_2 - 2a}{\alpha_1 + \alpha_2 - a}$	$\frac{b+c}{a+b+c}$	Colwell & Coddington (1994; 'complementarity' measure), see also Pielou (1984)
16	β_g	$\frac{b+c}{a+b+c}$	Gaston <i>et al.</i> (2001) ²
17	$\beta_{-3} 1 - \frac{\alpha_{\max}}{S}$	$\frac{\min(b,c)}{a+b+c}$	Williams (1996a)
18	$\beta_l S - \bar{\alpha}$	$\frac{b+c}{2}$	Lande (1996)
19	$\frac{r_s + 1}{(S^2 - S)/2}$	$\frac{bc + 1}{((a+b+c)^2 - (a+b+c))/2}$	Williams (1996a), Williams <i>et al.</i> (1999)
20	$\beta_{hk} 1 - \frac{2a}{\alpha_1 + \alpha_2}$	$1 - \frac{2a}{2a+b+c}$	Harte & Kinzig (1997) ³
21	β_{rib}	$\frac{a}{a+c}$	Ruggiero <i>et al.</i> (1998) ⁴

Continued overleaf

Table 1. *Continued*

	Original formulation	Measure re-expressed	Source
22	$\beta_{\text{sim}} 1 - \frac{a}{\min(b, c) + a}$	$\frac{\min(b, c)}{\min(b, c) + a}$	Lennon <i>et al.</i> (2001), based on Simpson (1943)
23	β_{gl}	$\frac{2 b - c }{2a + b + c}$	Lennon <i>et al.</i> (2001) ⁵
24	β_z From SAR	$1 - \left[\log \left(\frac{2a + b + c}{a + b + c} \right) / \log 2 \right]$	Lennon <i>et al.</i> (2001), see also Harte & Kinzig (1997) & Appendix

S = total number of species recorded for both quadrats ($S = a + b + c$); $\bar{\alpha}$ = average number of species found within the quadrats; α_1 = total number of species found in the focal quadrat; α_2 = total number of species found in the neighbouring quadrat; α_j = total number of species found in the quadrat j ; α_{max} = maximum value of species richness for the two quadrats; N = number of quadrats; r = number of species pairs whose distributions overlap; g = cumulative gain in species; l = cumulative loss in species; H = range of habitat gradient; e_i = number of quadrats under comparison in which species i is found; $T = \sum e_i = \sum \alpha_j$; C = species in common between two censuses; T_i = total number of species in census i ; r_s = number of cases in which there is no species overlap (number of unique pairwise species comparisons without co-occupancy of any quadrat); SAR = species–area relationship, $S = kA^z$, where S is species number, A is area and z and k are constants. The parameter z is a beta diversity measure based on species gain. See Appendix for derivation of β_z .

¹ $\beta_1 = \beta_2$ when $a = \alpha_{\text{max}}$.

²Originally formulated for five, four or three adjacent quadrats, for which β_g of the focal quadrat is the percentage of ‘transition species’ in relation to the total number of species found in the sequence of adjacent quadrats. The transitional species for a pair of quadrats were considered here as b and c .

³From definition of ‘turnover = 1 – commonality (the number of species in common divided by the average number of species in the two patches)’.

⁴Measure of assemblage similarity between quadrats calculated as ‘the proportion of species at this central point present at every one of the remaining cells’.

⁵Not intended to be a measure of ‘beta diversity’ *per se*, this was originally used to represent differences in species richness between quadrats, i.e. to provide a measure of local alpha diversity gradients.

THE MEASURES

The 24 measures of beta diversity considered are listed in Table 1. These comprise those measures that have been suggested or employed in recent analyses of patterns in beta diversity based on species presence/absence data. Other similarity or distinctness measures, of which there are many, that have not been used or proposed as suitable for this purpose are ignored; some of these may yet prove useful in the context of spatial turnover in species identities. Following the conventions established previously, the 24 measures are identified in terms of a subscripted ‘ β ’ using, where possible, those subscripts employed previously and indicating fresh ones where appropriate.

In each case, the original equations for the measures of beta diversity have also been re-expressed in terms of the pairwise matching/mismatching components used in similarity/dissimilarity coefficients, and usually denoted as a , b and c (e.g. Krebs 1999). Considering the simplest case, that of two equal-area quadrats, one can be regarded as the ‘focal quadrat’, and its species composition can be compared with that of the other, the ‘neighbouring quadrat’. The matching component a is the total number of species shared by the two quadrats (i.e. the number occurring in both), b is the number of species present in the neighbouring quadrat but not in the focal quadrat, and c is the number of species present

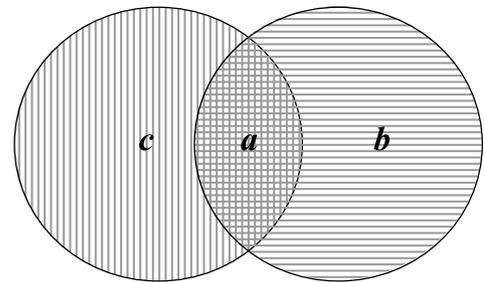


Fig. 2. The possible spatial distribution of a species across a pair of quadrats. (a) Component a comprises the total number of species that occur in both quadrats; (b) component b comprises the total number of species that occur in the neighbouring quadrat but not in the focal one; and (c) component c comprises the total number of species that occur in the focal quadrat but not in the neighbouring one.

in the focal quadrat but absent from the neighbouring quadrat (Fig. 2). The a component is thus the species in common for a pair of quadrats, while the b component measures species gain and the c component species loss relative to the focal quadrat. The re-expressed formulae in Table 1 are valid only for pairwise comparisons. Although the approach could be extended to multiple comparisons, pairwise ones remain the basis of the vast majority of published analyses of patterns in beta diversity and thus this constraint is not overly restrictive.

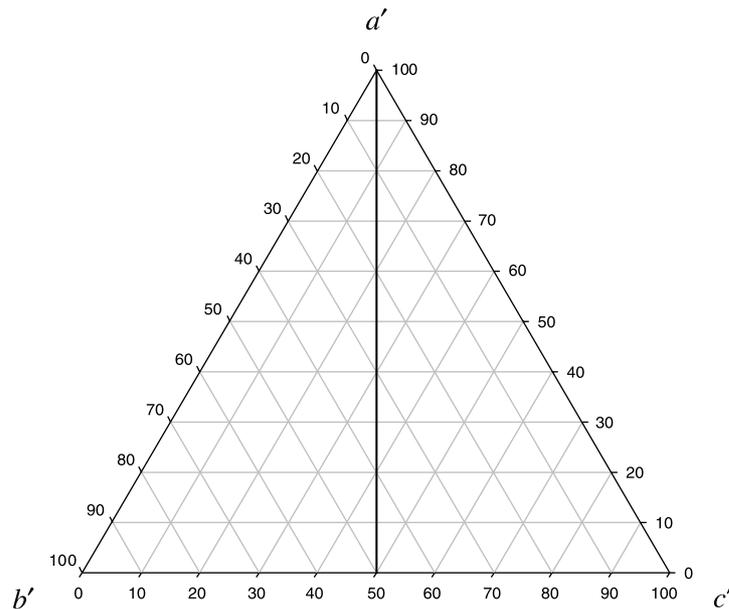


Fig. 3. Interpretation of ternary plots of the matching components a' , b' and c' . See text for further details.

Expressed in terms of matching/mismatching components and this simple scenario, it is clear that a wide range of the possible simple ways of combining a , b and c have been proposed at some time as measures of beta diversity (Table 1). Four pairs of the 24 measures are precisely the same for the case of a pair of quadrats [$\beta_w = \beta_{-1}$ (if the former is formulated with subtraction of a constant), $\beta_t = \beta_{me}$, $\beta_c = \beta_l$, $\beta_{cc} = \beta_{gl}$], and $\beta_j = 1 - \beta_{cc}$. In addition, β_{wb} is the same as β_c multiplied by a constant. Our analysis is therefore restricted to the remaining 18 measures of beta diversity.

THE SIMPLEST CASE

For the purpose of comparing the properties of the 18 measures, we consider first the contribution to each of the three matching components for a pair of quadrats, the focal and the neighbouring (the most common basis in the literature for calculating beta diversity). In order that this would be independent of variation in the overall numbers of species, we conducted the comparisons in terms of a' , the percentage of species shared by the pair of quadrats, b' , the percentage of species present exclusively in the neighbouring quadrat, and c' , the percentage of species present only in the focal quadrat. The total number of species for the pair of quadrats is $a + b + c$, and therefore $a' + b' + c' = 100\%$. The species richness for the focal quadrat (i.e. alpha diversity, α) equals the total number of species common to both quadrats plus those present exclusively in this quadrat, that is, $a + c$, which is represented by $a' + c'$ (this being negatively correlated with b' , $r = -1$); the equivalent expression for the neighbouring quadrat is $a' + b'$ (negatively correlated with c' , $r = -1$); of course, values of a , b and c are not necessarily correlated in this manner (Lennon *et al.* 2001). We analyse all possible combina-

tions of integer percentages of species among the three components, and use ternary plots to examine the relationship between these and beta diversity values (Figs 3 and 4). The degree of shading in each plot represents (on an equal interval scale) the value of a given beta diversity measure (darker shading for larger values for dissimilarity measures, lighter shading for similarity measures, see below), relative to the values of a' , b' and c' (each of which increase in the direction of the appropriate letter at the corners of the plot). The magnitude of a' , the degree of species continuity between the two quadrats increases from the base of the plot towards its apex, and for a given value of a' the lateral position of a point reflects the relative contribution of species gains (b') and losses (c') (Fig. 3). The displacement of a point from a vertical line between the base and the apex of the triangle (i.e. $b' - c'$) reflects the difference in alpha diversity between the two quadrats.

Similar empirical spatial patterns of variation in beta diversity have been observed for β_{-1} and β_t when these are applied to the same data sets (Wilson & Shmida 1984; Blackburn & Gaston 1996). Under the above conditions, β_{-1} and β_t were not identical for a pair of samples (Wilson & Shmida 1984); however, by definition they are obviously linearly dependent and using a' , b' and c' values were perfectly positively correlated ($r = 1$). Such linear relationships are also expected by definition (Table 1) between other measures, such as β_t and β_{sor} (Mourelle & Ezcurra 1997) and β_{sor} and β_{hk} , which are perfectly negatively correlated ($r = -1$), as are therefore β_{sor} and β_{-1} . Other pairs of measures showing perfect negative correlations are $\beta_j - \beta_c$, and $\beta_j - \beta_{cc}$, while $\beta_t - \beta_{hk}$, and $\beta_c - \beta_{cc}$ are perfectly positively correlated ($r = 1$).

Intuitively, when viewed as indices of similarity, measures of beta diversity for presence/absence data

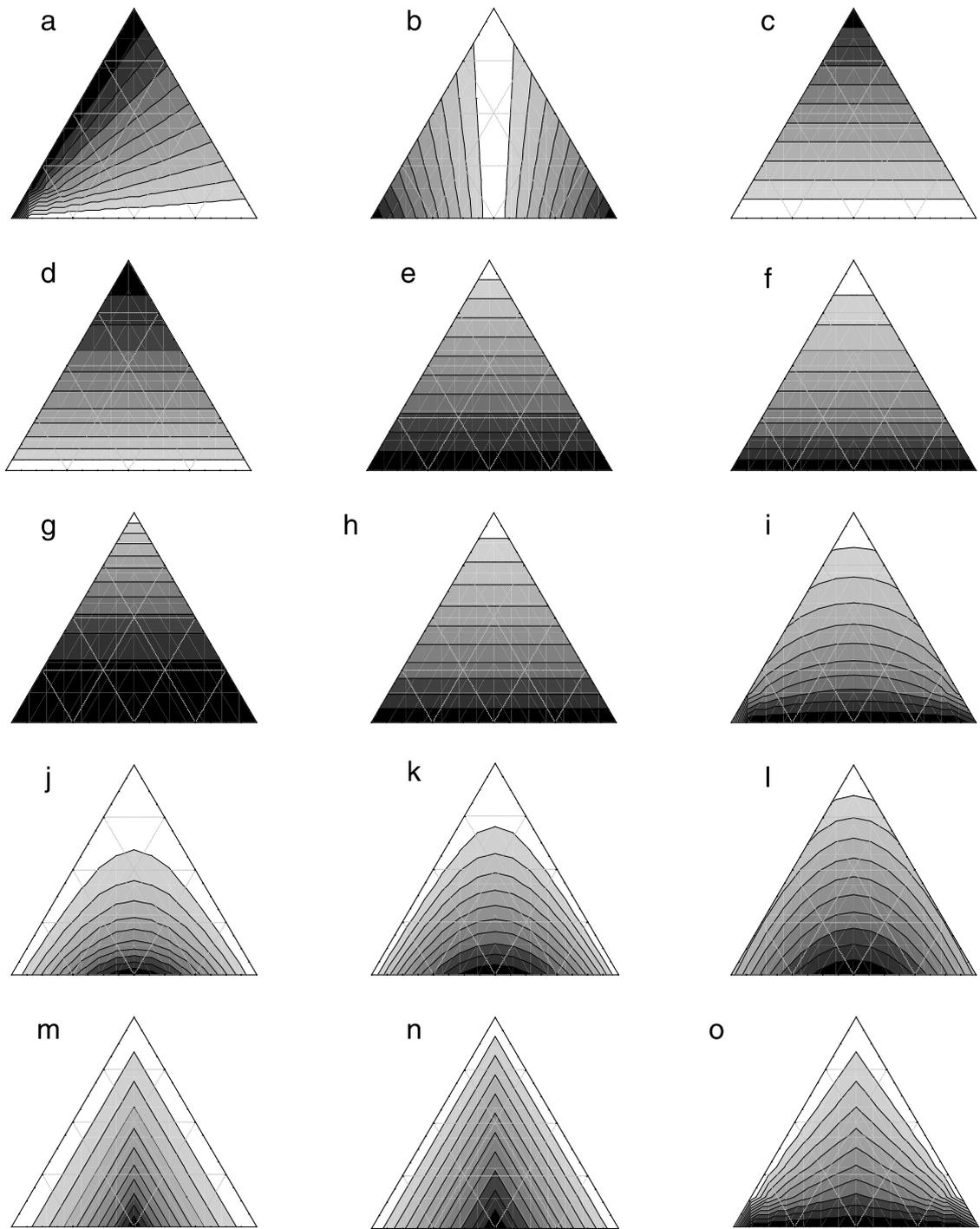


Fig. 4. Patterns of variation in the values of beta diversity [shading on an equal interval scale, from low (white) to high (black)] for pairwise comparisons between two hypothetical quadrats for all combinations of integer percentages of the turnover components a , b and c on a percentage scale (i.e. a' , b' and c'). (a) β_{tib} , (b) β_{gl} , (c) β_j , (d) β_{sor} , (e) β_c , (f) β_w , β_{hk} and β_t , (g) β_m , (h) β_z , (i) β_{co} , (j) β_r , (k) β_{rs} , (l) β_1 and β_e , (m) β_{-2} , (n) β_{-3} and (o) β_{sim} .

might be expected to exhibit minimum and maximum values of 0 and 1, respectively, or some simple function thereof. As some measures are cast in terms of dissimilarity and some in terms of similarity, an increase in the value of a measure can mean either an increase in turnover (dissimilarity) or a decrease (similarity). Thus, if such an intuitive property were to hold, beta diversity should have minimum possible values of zero

(dissimilarity measures) or maximum possible values of one (similarity measures), when there is no similarity between the species composition of the two quadrats, and maximum possible values of one (dissimilarity measures) or minimum values of zero (similarity measures) when their species composition was identical using a' , b' and c' . Several of the measures considered here scale rather differently from this, both in that they

Table 2. The maximum and minimum possible values of the beta diversity measures tested, and the conditions under which they occur. These are calculated by expressing the matching components a , b and c as percentages of the total number of species found in a pair of quadrats (a' , b' and c' ; see text for details). ‘–’ indeterminate values. For β_w and β_r values when corrected with -1 (see Table 1) are included in parentheses

Measure	Minimum	a'	b'	c'	Maximum	a'	b'	c'
β_{rib}	0 –	0 0	< 100 100	> 0–100 0	1	> 0–100	< 100	0
β_{gl}	0	100	0	0	2	0	>> 0 >> 100	>> 100 >> 0
β_j	0	0	0–100	0–100	1	100	0	0
β_{sor}	0	0	0–100	0–100	1	100	0	0
β_w	1 (0)	100	0	0	2 (1)	0	0–100	0–100
β_c	0	100	0	0	50	0	0–100	0–100
β_t	0	100	0	0	1	0	0–100	0–100
β_{hk}	0	100	0	0	1	0	0–100	0–100
β_z	0	100	0	0	1	0	0–100	0–100
β_m	0	100	0	0	100	0	0–100	0–100
β_{co}	0	100	0	0	– – 1	0 0 0	100 0 0–< 100	0 100 0–< 100
β_r	1 (0)	0–100 0–100	0 0–100	0–100 0	2 (1)	0	50	50
β_i	0 – –	100 0 0	0 100 0	0 0 100	0.30103	0	50	50
β_e	0 – –	100 0 0	0 100 0	0 0 100	0.35125	0	50	50
β_{rs}	0.0002020	0–100 0–100	0 0–100	0–100 0	0.50525	0	50	50
β_{-2}	0	0–100 0–100	0 0–100	0–100 0	1	0	50	50
β_{-3}	0	0–100 0–100	0 0–100	0–100 0	0.5	0	50	50
β_{sim}	0	0–100 0–100	0 0–100	0–100 0	– – 1	0 0 0	100 0 0–100	0 100 0–100

do not attain these maximum and minimum values, and in that they do not do so under these particular conditions (Table 2; see Wolda 1981 for a similar finding for similarity indices). Both β_w and β_r vary from 0 to 1 or from 1 to 2, depending on whether they are corrected by -1 , providing the same scale of variation, as does β_M , which varies from 0 to 100. However, there are other cases when the minimum value is zero but the maximum value is not 1 (for β_{gl} , β_c , β_r , β_e and β_{-3}), and one in which neither is so (β_{rs}) (Table 2). As long as limits are finite, maximum and minimum values can be normalized to the unit interval (this re-scaling and comparability is achieved in effect by the graphical scaling system in Williams 1996a; Williams *et al.* 1999). However, as formulated originally (or in terms of a , b and c), for some of the measures finite limits may be difficult to define.

On the basis of their responses to variation in the percentages of the three matching components (a' , b' and c'), four groups of measures of beta diversity can be distinguished. For convenience, we term these (1) measures of continuity and loss – β_{rib} ; (2) measures of species richness gradients – β_{gl} ; (3) measures of continuity – β_j , β_{sor} , β_w , β_c , β_t , β_{hk} , β_z , β_m ; and (4)

measures of gain and loss – β_{co} , β_r , β_i , β_e , β_{rs} , β_{-2} , β_{-3} , and β_{sim} .

(i) Measures of continuity and loss

One of the 24 measures analysed, β_{rib} , depends solely on the values of a and c (Fig. 4a). This measure returns values of zero (total dissimilarity) when no species are shared between two quadrats ($a' = 0$), and values of 1 (total similarity) when $c' = 0$ (Table 2). When values of a' and c' are low, then the value of β_{rib} is very sensitive to small changes in c' (Fig. 4a).

(ii) Measures of species richness gradients

Values of β_{gl} depend on the difference in species richness between the two quadrats under consideration (Fig. 4b). This measure has been employed previously to test if the values of other measures of beta diversity serve simply to recover patterns in local species richness gradients (Lennon *et al.* 2001). When the matching component a' equals zero, minimum values of β_{gl} are observed when the two quadrats have the same species richness, that is b' and $c' = 50$ (Fig. 5d). When

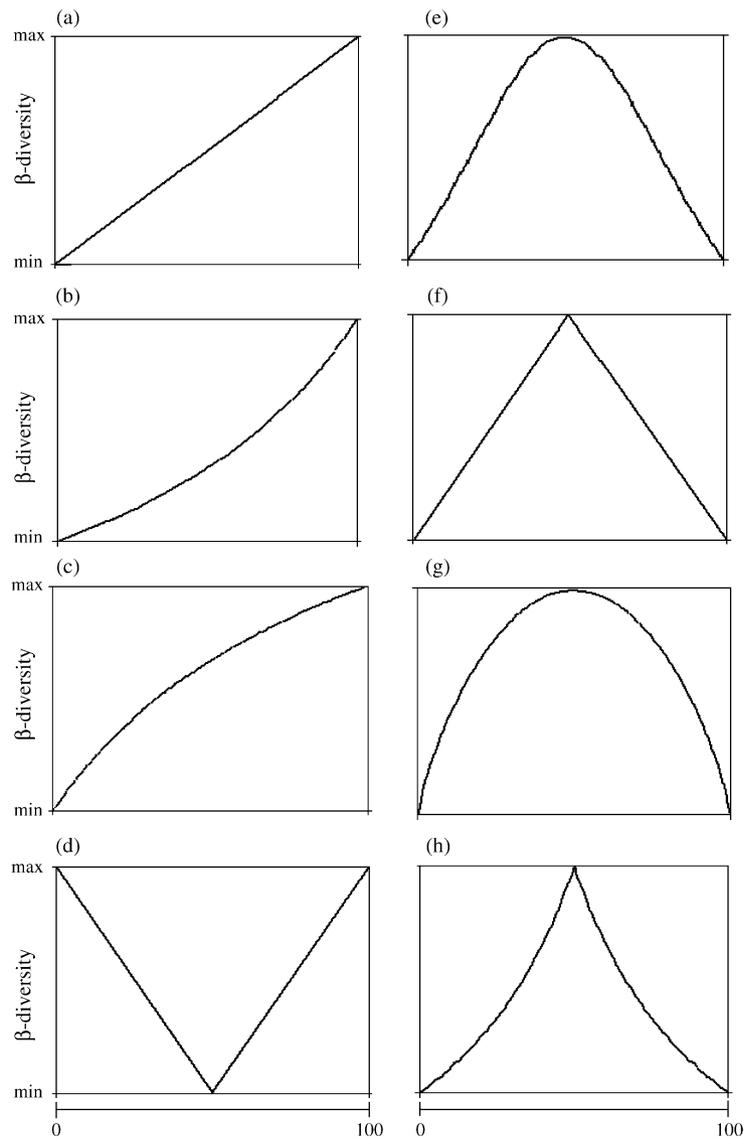


Fig. 5. Patterns of beta diversity for a hypothetical pair of quadrats considering all different possible integer percentages of two turnover components when the third component is zero (i.e. a , b , or $c = 0$). The x axis represents values of one of the two non-zero components – when the other non-zero component equals 100 minus this value – and the y axis the values of beta diversity. See text for details of the cases in which each beta diversity measure exhibits one of the illustrated patterns.

either component b or c is zero there is a curvilinear increase in the value of β_{gl} (Fig. 5b).

(iii) Measures of continuity

The values of several measures of beta diversity are dependent essentially on variation in the matching component a , the level of continuity in species composition between two quadrats. Such measures will always tend to assume extreme values (high or low depending on the direction of scaling with a) when differences in the richness between the focal and the neighbouring quadrat are large – because a will then tend to be small, i.e. b or c are large relative to a . This group of measures reflects what we term ‘broad-sense’ turnover, which implicitly incorporates differences in composition attributable to diversity gradients, but

ignores the relative magnitude of species gains and species losses.

There are two groups of measures whose values are related directly to variation in the matching component a . Values for the first group all scale positively with increases in a . These are β_j and β_{sor} (Fig. 4c,d), which are well known as similarity indices, because of this dependence on a . High values are interpreted as reflecting low beta diversity (high similarity), and low values as reflecting high beta diversity (high dissimilarity).

The second group of measures whose values show simple relations to variation in a all scale negatively with increases in this matching component. These are β_c , β_w , β_{hk} , β_t , β_m and β_z (Fig. 4e–h). β_w is the most widely used measure of beta diversity in ecology (Fig. 1b, e.g. Routledge 1977, 1984; Wilson & Shmida 1984; Weiher & Boylen 1994; Blackburn & Gaston

Table 3. Performance of the measures of beta diversity analysed under different criteria (see text for details). The nested quadrats criterion used here is that turnover is minimized when $c' = 0$. '√' – criterion is fulfilled, and '–' – criterion is not fulfilled. In a few instances, β_w and β_j only fulfil criteria with the –1 correction (see Table 1)

Measure	Symmetry	Homogeneity	Nested quadrats	Additivity
β_{rib}	–	√	√	–
β_{gl}	√	√	–	–
β_j	√	√	–	–
β_{sor}	√	√	–	–
β_w	√	√	–	–
β_c	√	–	–	–
β_t	√	√	–	–
β_{hk}	√	√	–	–
β_z	√	√	–	–
β_m	√	–	–	–
β_{co}	√	√	–	–
β_r	√	√	√	–
β_i	√	√	–	–
β_e	√	√	–	–
β_{rs}	√	–	√	–
β_{-2}	√	√	√	–
β_{-3}	√	√	√	–
β_{sim}	√	√	√	–

1996; Harrison 1997; Mourelle & Ezcurra 1997; Clarke & Lidgard 2000; Koleff & Gaston 2001). However, following the criticisms of this measure by Wilson & Shmida (1984; see below), increasing use has been made of β_i (Fig. 1b, e.g. Willig & Sandlin 1992; Blackburn & Gaston 1996; Mourelle & Ezcurra 1997; Willig & Gannon 1997; Koleff & Gaston 2001). β_z is derived from the species–area relationship (Table 1), which implicitly considers information about species turnover (Harte & Kinzig 1997).

The values of the nine measures of beta diversity based on species continuity show rather different patterns of change when either components b or c are zero. β_j and β_c , which are based on the average change in species composition between quadrats, have linear relationships (Fig. 5a), while curvilinear increases are shown by β_w , β_{hk} , β_i and β_z (Fig. 5b), and concave relationships by β_{sor} and β_m (Fig. 5c).

(iv) Measures of gain and loss

Values of the final group of measures of beta diversity, β_{co} , β_r , β_i , β_e , β_{rs} , β_{-2} , β_{-3} and β_{sim} , depend on a and on the relative magnitude of b and c . These can be considered as 'narrow-sense' measures of turnover, in that they focus on compositional differences more than differences in species richness. While values of these measures all increase with declines in component a' , they also peak at intermediate values of b' and c' (Fig. 4i–o), and attain their maximum values when the percentage of species shared in common between the focal and neighbouring quadrats is small and the percentages gained and lost in moving from the focal to the neighbouring quadrat are similar.

The values taken by β_r , β_i , β_e and β_{rs} reflect the degree of overlap of species distributions, and thus the 'r'

parameter proposed by Routledge (1977; Table 1). These all exhibit a curvilinear pattern of change in their values, with changes in the relative magnitudes of b' and c' . The values of β_{-2} and β_{-3} exhibit a triangular pattern of change, while those of β_{sim} follow a similar pattern at high values of a' but become highly sensitive to small changes either in b' or c' when values of a' and either b' or c' are low.

When there are no species in common between the two quadrats ($a' = 0$), the pattern of change in the value of beta diversity with variation in the other two matching components differs between measures. It is hump-shaped for β_r (Fig. 5e) and β_i , β_e and β_{rs} (Fig. 5g), and exhibits a triangular pattern for β_{-2} (Fig. 5h) and β_{-3} (Fig. 5f). Under this circumstance, β_{sim} assumes a constant value of 1, regardless of variation in the matching components b and c .

OTHER SIMPLE PROPERTIES

We tested three further simple properties that beta diversity measures might be expected to possess (Table 3).

(i) Symmetry

For many purposes, for two quadrats x and y , a beta diversity measure $\beta(x, y)$ must be equal to $\beta(y, x)$. That is, beta diversity should be symmetric with regard to variation in the matching components b and c (Janson & Vegelius 1981). In other words, if we exchange the neighbouring and focal quadrat identities the measure should remain unchanged if symmetric. All measures satisfy this criterion, except for β_{rib} (Table 3).

(ii) Homogeneity

If all the matching components, a , b and c are multiplied by the same constant, this should not affect the

value of the measure of beta diversity. That is, beta diversity should be independent of the total number of species as long as the proportions comprising the different components are constant (Janson & Vegelius 1981). This criterion is fulfilled by all of the measures when re-expressed in terms of the matching components, except for β_{co} , β_c and β_m , although for the last two multiplying the matching components by a constant multiplies the measure by the same constant (Table 3).

(iii) *Nested quadrats*

Quadrats may be nested physically, such that the focal quadrat lies entirely within the neighbouring quadrat, and all the species occurring in the former also occur in the latter. If all the species in the neighbouring quadrat also occur in the focal quadrat ($b = c = 0$), then there should be no turnover, and beta measures should attain either their minimum or maximum values depending on the direction in which they scale (Wilson & Shmida 1984). This condition is met by all of the measures considered here. If all of the species in the focal quadrat are also found in the neighbouring quadrat ($c = 0$), but the neighbouring quadrat has species not found in the focal quadrat ($b > 0$), then one would expect that there should be no turnover if this equates to gain and loss, independently of how of large or small is the percentage of species that the two quadrats have in common. For all the measures whose values depend on b and c , minimum species turnover is detected if either of those components become zero, except for β_{co} , β_l , and β_e (Table 3).

INCREASING COMPLEXITY

Thus far, with the exception of nestedness, we have considered the simplest case, that of a single pair of adjacent equal-area quadrats. In practice, there are many other situations in which measures of beta diversity are

applied. Although typically they remain based on pairwise comparisons, they commonly bring with them additional considerations.

(i) *Transects*

When beta diversity is calculated along transects several concerns arise. The first is the sensitivity of measures to local gradients in species richness. This is a particular problem for measures that scale essentially with variation in a , the number of species in common to a given pair of quadrats (measures of continuity). As observed above, these will tend to assume extreme values (high or low depending on the direction of scaling with a) when differences in the richness between the focal and the neighbouring quadrat are large – because a will then tend to be small.

Secondly, the additivity of measures of beta diversity may become important in the context of transects (Wilson & Shmida 1984). For the simplest case of three quadrats in the spatial sequence x, y, z , a measure will be additive if the sum of the values of beta diversity between x and y and between y and z equals the value of beta diversity between x and z . The additivity exhibited by some measures depends on the patterns of species richness in the quadrats along the transect (Wilson & Shmida 1984; Magurran 1988) and also on whether or not the species distributions are nested. Here we consider whether the additivity criterion is met for four different hypothetical situations along a transect of three contiguous quadrats (Fig. 6).

None of the 18 measure of beta diversity is completely additive for all of the cases tested (Table 3; see Wilson & Shmida 1984; Magurran 1988); most measures fail the test of additivity under most of the cases examined.

To study the pattern of spatial turnover along a gradient, a number of different approaches have been used, and the distinctions between them are important,

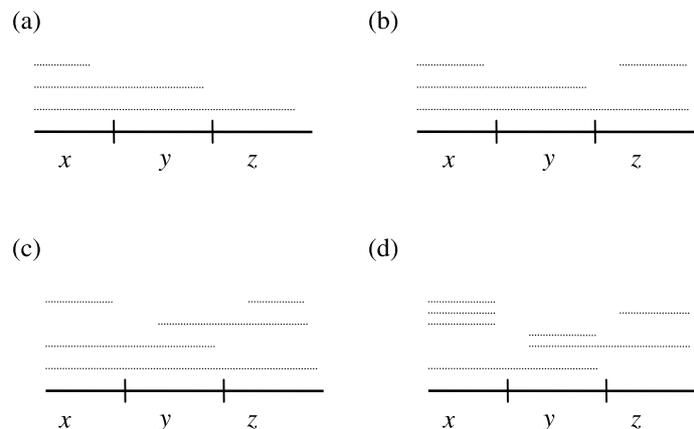


Fig. 6. Four hypothetical cases used to evaluate the additivity property. Species distribution along three quadrats, x, y, z , within a transect are represented by dashed lines. (a) Nested quadrats with different species richness, α . (b) Different α among quadrats. (c) Equal α among quadrats. (d) Different α among quadrats and $a = 0$ between extreme quadrats. If a measure exhibits the additivity property, then beta diversity of the complete transect, $\beta(x,z)$ equals the sum of beta diversity between each pair of contiguous samples along the gradient, $\beta(x,y) + \beta(y,z)$.

irrespective of the actual measures of beta diversity employed. First, beta diversity has been calculated between adjacent pairs of quadrats along a transect, and the relationship sought between these values and the position on the transect (Wilson & Shmida 1984; Cody 1986), or a single value has been obtained from the cumulative gain and loss of species from the pairwise comparisons (Willig & Sandlin 1992; Blackburn & Gaston 1996; Mourelle & Ezcurra 1997). Secondly, beta diversity has been calculated between all pairs of quadrats along the transect, and the relationship sought between these values and the distance separating each of the pairs (Whittaker 1960, 1972; Cody 1986; Harrison *et al.* 1992; Mourelle & Ezcurra 1997; Clarke & Lidgard 2000) or the beta diversity between the pairs is expressed graphically, grouping similar areas (Magurran 1988; Price *et al.* 1999). Species turnover often depends on the distance between the quadrats compared, with low to moderate values typically expected over short distances and higher levels over longer distances (Cody 1986; Harte & Kinzig 1997). Thirdly, beta diversity is estimated for the whole transect on the basis of the relationship between the species richness of the quadrats and the overall richness of the whole transect (Whittaker 1960; Wilson & Shmida 1984; Harrison *et al.* 1992; Blackburn & Gaston 1996).

A fourth possible approach involves direct comparison of the extremes of the transect, effectively assuming that a species present at both extremes is continuously present between them, even though it may actually be absent from intermediate quadrats. However, such assumptions may produce unsatisfactory results (Whittaker 1960; Wilson & Shmida 1984).

(ii) Grid systems

In the case of grid systems, beta diversity can be evaluated for a focal quadrat relative to that of its multiple

neighbours. Consider a grid of equal area quadrats with a central focal cell and the eight surrounding neighbours. Values of the matching components a , b and c could be calculated between the focal cell and each neighbour, and then the average of these values used to calculate beta diversity. Alternatively, the matching components could be used to calculate eight values of beta diversity and these could then be averaged (Williams 1996a; Lennon *et al.* 2001). In both cases, corrections can be made readily where data are missing, or unavailable, for some neighbours.

These two methods will give the same results, except for measures of beta diversity that are based on maximum or minimum values of any component, such as β_{-2} , β_{-3} and β_{sim} . We contrasted both approaches for β_{sim} , using data for the breeding birds of South-east Scotland (Murray *et al.* 1998), and based on the occurrences of 125 species across 1756 grid cells of 2×2 km (using Worldmap in the calculation of values of beta diversity; Williams 1996b). The values for the two methods of analysis were positively correlated ($r = 0.849$, $n = 1756$, $P < 0.0001$); none the less, because the minimum value of b or c is considered in the formulation of β_{sim} (see Table 1), higher values of beta diversity result using the first method (Fig. 7).

An alternative approach may be to estimate beta diversity from the matching components for the focal quadrat compared with the composition of the entire set of neighbours, treating them as a single unit (Williams 1996a). This results in the comparison of focal and neighbouring areas of different size, which is often undesirable. It builds a strong asymmetry into the values of b and c ; species gains are magnified relative to species losses, compared with the case of equal-sized quadrats. Using the South-east Scotland breeding birds data a weak relationship exists between the values of β_{sim} obtained with this methodology and those generated by averaging across each of the pairwise comparisons between the focal and neighbouring quadrats

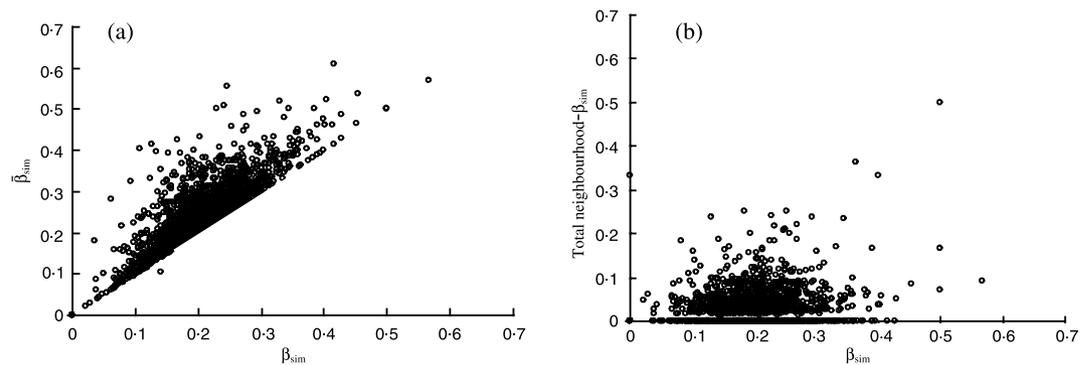


Fig. 7. Relationships between the values of beta diversity obtained using three different methods, for the breeding birds of South-east Scotland (see text for details) considering a nine-quadrat neighbourhood in a grid system. β_{sim} (x axis in both cases) was obtained by averaging values of beta diversity for the focal quadrat and each neighbouring quadrat. (a) β_{sim} was estimated from the average values of the matching components a , b and c between the focal quadrat and each quadrat in the neighbourhood. (b) β_{sim} –total neighbourhood- β_{sim} is the pairwise comparison of the matching components between the focal quadrat and all the neighbouring quadrats considered as a single unit.

($r = 0.135$, $n = 1756$, $P < 0.001$). Lower values were generally observed when treating the neighbourhood as a single unit and different focal quadrats were highlighted as areas of low or high spatial turnover using the different approaches (Fig. 7).

A novel approach to evaluating beta diversity (although not a novel measure) for data on grid systems, was suggested recently by Gaston *et al.* (2001). β_g was estimated across transects in four different directions (W–E, N–S, NW–SE and NE–SW), and the maximum value was attributed to the central focal quadrat. This methodology could be used for other measures. However, it was intended to detect areas with high species replacement when data are fragmented because of variable sampling effort (see also Williams *et al.* 1999). The main problem for this approach is that it will find high beta diversity when differences in alpha diversity are large, i.e. choosing the maximum biases the measure towards pairs of quadrats differing in alpha diversity. A minor weakness is also that the area of contact among the focal and the neighbouring cells is larger for the vertical (N–S) and the horizontal (W–E) comparisons than for the two diagonals (NW–SE, NE–SW); the Euclidean distance between the centres of the focal and each surrounding quadrat is different in the diagonal directions than in the vertical or horizontal directions. This might increase the probability of finding a species on two contiguous quadrats for the N–S and W–E lines.

(iii) Unequal numbers of areas

It is not unusual for a single value of beta diversity to be calculated across multiple areas, and this value compared with those generated from other such sets of areas (e.g. values are calculated across quadrats within each of several latitudinal bands and used to assess whether beta diversity changes with latitude; Willig & Sandlin 1992; Blackburn & Gaston 1996; Clarke & Lidgard 2000). Seldom in such cases is the number of areas used to calculate each value of beta diversity constant (e.g. latitudinal bands differ in their longitudinal span). This means effectively that beta diversity is being calculated over total areas of different sizes, which can strongly bias the resulting values.

Some of the measures of β -diversity listed in Table 1 were formulated with the explicit intention of correcting for biases caused when comparing different numbers of areas. Thus, the division by the number of quadrats ($N - 1$) in the formulation of β_{-1} and β_{-2} by Harrison *et al.* (1992), and of β_{me} by Mourelle & Ezcurra (1997) (Table 1) was suggested to address the problem of variation in transect length. Unfortunately this constitutes an over-correction, because the exponent of the species–area relationship is typically much less than 1 and may lead to beta diversity becoming negatively correlated with the number of quadrats.

Without correction, the comparison of beta diversities calculated for different numbers of quadrats or

different-sized areas will inevitably bias results. The extent to which this effect is sufficient to obscure real biological patterns remains unknown, but it is clearly undesirable.

(iv) Unequal spatial scale

Measures of beta diversity have been used to evaluate spatial turnover at many different scales. Units of study vary from a few square metres (e.g. Whittaker 1960; Routledge 1977; Wilson & Shmida 1984; Pharo, Beattie & Binns 1999) to tens and hundreds of square kilometres (e.g. Cody 1986; Harrison *et al.* 1992; Willig & Sandlin 1992; Blackburn & Gaston 1996; Poynton & Boycott 1996; Williams 1996a; Price *et al.* 1999; Clarke & Lidgard 2000; Koleff & Gaston 2001). Changing spatial scale (quadrat size) is likely to change spatial patterns in beta diversity, with the matching component a often tending to increase as spatial resolutions become coarser (Lennon *et al.* 2001). In consequence, the values of some measures of beta diversity are likely to increase with spatial scale and those of others to decrease. This may create difficulties for the comparison of patterns in turnover reported by studies performed at different scales, although the extent to which differences in the behaviour of turnover are solely a result of scale is unknown.

(v) Comparing assemblages with different rank–occupancy distributions

Finally, measures of beta diversity have been employed to examine patterns of turnover in assemblages with different underlying occupancy structures; some may have many restricted species and few widespread ones, and others the converse (differences in the shape of species–occupancy distributions is partly a function of spatial scale; Gaston 1994; Gaston & Blackburn 2000). Assemblages with high proportions of widely and narrowly distributed species will, respectively, tend to exhibit low and high levels of beta diversity. Thus, splitting the breeding birds of South-east Scotland into two groups, the 50% with the lowest and the 50% with the highest levels of tetrad occupancy, reveals that the former sample a much broader spectrum of potential values of turnover than do the latter (Fig. 8). Hence, in the case of an assemblage of relatively restricted species, turnover will depend more strongly on the behaviour of the measure of beta diversity across the entire range of the matching components, and is likely to be influenced more by differences in species richness between quadrats if these are not explicitly taken into account. Moreover, comparative studies of beta diversity between different assemblages or different study areas may, for the most part, detect differences in the overall commonness and rarity of species. It may be desirable, in some instances, to develop ways of allowing for this effect, such that the element of turnover not solely attributable to commonness and rarity differences can be studied.

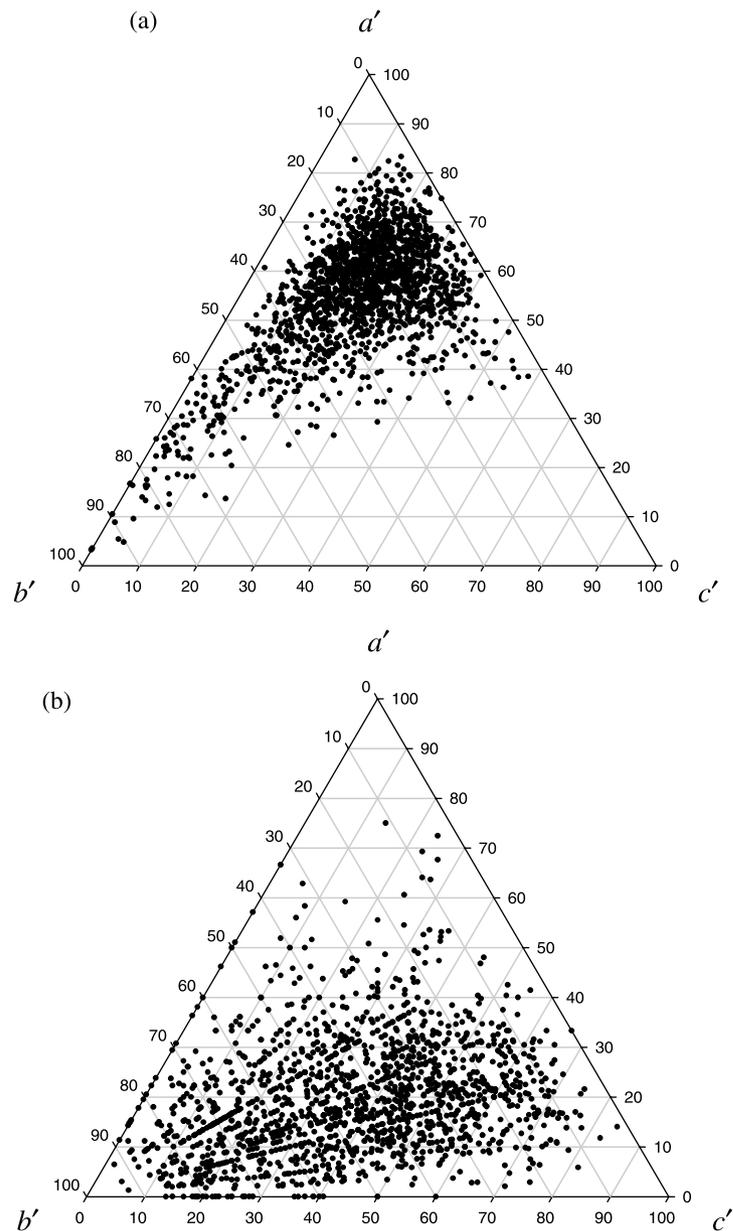


Fig. 8. Scatter plots in a' , b' and c' space for the breeding birds of South-east Scotland (see text for details) for (a) the 50% most widespread, and (b) the 50% most restricted species. Values are the averages for each cell when compared with its eight neighbouring tetrads (or less at the limits of the study area). The scatter of points for these data suggests low numbers of species distributed exclusively in a focal quadrat in relation to its neighbourhood; that is, b' is consistently larger than c' .

Conclusions

A broad range of measures has been employed to express variation in beta diversity. Perhaps most importantly this suggests a fundamental lack of agreement in the literature as to the feature of the pervasive spatial turnover in the identities of species that beta diversity is intended to capture. Not only do different groups of these measures based on presence/absence data scale with different matching components, but within each of these groups the pattern of scaling is often very variable (Figs 4 and 5). Great caution must clearly be exercised in comparing the results of studies that have used different measures of beta diversity,

and in many instances no direct comparison will be possible.

The eight measures of beta diversity that reflect gain and loss (β_{co} , β_r , β_l , β_e , β_{-2} , β_{-3} , β_{rs} and β_{sim}) capture the notion that turnover is high when the proportion of species shared between two quadrats is low and the proportions lost and gained moving from one to the other are similar; that is they take into account differences caused by unequal numbers of species. This seems to be how measures of beta diversity are commonly intended to behave. Unfortunately, none of these eight measures meets all of the criteria against which their performance was tested. All fail the test of additivity under at least some of the simple scenarios

explored, although β_{sim} , for example, meets this test under most (Table 3). Moreover, these measures show considerable differences in the shape of the surface relating variation in a' , b' and c' (Fig. 4). On balance, of these measures β_{sim} perhaps performs best overall. Certainly one of these eight measures is likely to be suitable for use in many studies of patterns in beta diversity, although no single measure is likely to be appropriate in all circumstances.

The bulk of published analyses of beta diversity have not used gain and loss measures (Fig. 1b), but rather have used those that are sensitive particularly to variation in the continuity matching component, a . That is, they have concentrated on the level of sharing of species between areas, and have ignored the pattern of gains and losses. Aside from the fact that many of these measures have several undesirable properties (Table 3), this seems a rather restricted view of turnover. For example, consider two situations, in the first of which all those species not common to quadrats x and y are found only in quadrat x ; and in the other, while the same proportion of species as before are common to both quadrats, the remaining species are divided equally between quadrat x and quadrat y . It is difficult to conceive that these contrasting situations should be treated as equivalent. Narrow sense measures of beta diversity should at least be employed alongside broad sense measures, to improve the insight obtained into compositional change.

Consideration of measures of beta diversity in terms of matching components should also be strongly encouraged, particularly given that patterns in each of these components may provide a quick route to understanding why beta diversity is behaving in a given fashion and, more importantly, some of the fundamental features giving rise to patterns of variation in species composition. Calculation of beta diversity on this basis provides a standard for comparisons that has hitherto been largely absent, especially where levels of species richness have been markedly different. In that sense, measures that exhibit the homogeneity property in all circumstances are clearly superior. Where measures of beta diversity reveal different patterns of variation when based on absolute and proportional species numbers we recommend that both be explored.

Ternary plots may provide a useful tool in understanding and comparing values of beta diversity, both for existing and any new measures, with respect to values of the three matching components. In particular, this will provide insight into the areas of the parameter space defined by the three components that are occupied by an assemblage, and for some measures (e.g. Fig. 4b) the importance of differences in species richness in generating the patterns of beta diversity that are observed. However, the use of such plots based on a' , b' and c' does effectively reduce the three pieces of information to two (because they must sum to 100, in the case of percentages).

Finally, attention needs to be paid to the method by

which any given measure of beta diversity is calculated in the cases of transects and grid systems, or their equivalents. Several different approaches will usually be available, under at least some circumstances these may lead to different areas being identified as having high spatial turnover, and it will not always be obvious which approach is to be preferred.

Generalizations about patterns in beta diversity have thus far proved difficult to assess. A more rigorous and consistent approach to their description is an important first step.

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References

- Blackburn, T.M. & Gaston, K.J. (1996) The distribution of bird species in the New World: patterns in species turnover. *Oikos*, **77**, 146–152.
- Blackburn, T.M. & Gaston, K.J., eds (2003) *Macroecology: concepts and consequences*. Blackwell Science, Oxford.
- Brown, J.H. (1995) *Macroecology*. University of Chicago Press, Chicago.
- Brown, J.H. & Lomolino, M.V. (1998) *Biogeography*, 2nd edn. Sinauer Associates, Sunderland, Massachusetts.
- Clarke, A. & Lidgard, S. (2000) Spatial patterns of diversity in the sea: bryozoan species richness in the North Atlantic. *Journal of Animal Ecology*, **69**, 799–814.
- Cody, M.L. (1975) Towards a theory of continental species diversities: bird distributions over Mediterranean habitat gradients. *Ecology and Evolution of Communities* (eds M.L. Cody & J.M. Diamond), pp. 214–257. Belknap Press, Harvard.
- Cody, M.L. (1986) Diversity, rarity, and conservation in Mediterranean-climate regions. *Conservation Biology* (ed. M.E. Soulé), pp. 122–152. Sinauer Associates, Sunderland, Massachusetts.
- Cody, M.L. (1993) Bird diversity components within and between habitats in Australia. *Species Diversity in Ecological Communities: historical and geographical perspectives* (eds R.E. Ricklefs & D. Schluter), pp. 147–158. University of Chicago Press, Chicago.
- Colwell, R.K. & Coddington, J.A. (1994) Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society, London B*, **345**, 101–118.
- Dice, L.R. (1945) Measures of the amount of ecological association between species. *Ecology*, **26**, 297–302.
- Gaston, K.J. (1994) *Rarity*. Chapman & Hall, London.
- Gaston, K.J. (2000) Global patterns in biodiversity. *Nature*, **405**, 220–227.
- Gaston, K.J. & Blackburn, T.M. (2000) *Pattern and Process in Macroecology*. Blackwell Science, Oxford.
- Gaston, K.J., Rodrigues, A.S., van Rensburg, B.J., Koleff, P. & Chown, S.L. (2001) Complementary representation and zones of ecological transition. *Ecology Letters*, **4**, 4–9.

- Gaston, K.J. & Williams, P.H. (1996) Spatial patterns in taxonomic diversity. *Biodiversity: a biology of numbers and difference* (ed. K.J. Gaston), pp. 202–229. Blackwell Science, Oxford.
- Harrison, S. (1997) How natural habitat patchiness affects the distribution of diversity in Californian Serpentine Chaparral. *Ecology*, **78**, 1898–1906.
- Harrison, S., Ross, S.J. & Lawton, J.H. (1992) Beta diversity on geographic gradients in Britain. *Journal of Animal Ecology*, **61**, 151–158.
- Harte, J. & Kinzig, A.P. (1997) On the implications of species-area relationships for endemism, spatial turnover, and food web patterns. *Oikos*, **80**, 417–427.
- Jaccard, P. (1912) The distribution of the flora in the alpine zone. *New Phytologist*, **11**, 37–50.
- Janson, S. & Vegelius, J. (1981) Measures of ecological association. *Oecologia*, **49**, 371–376.
- Koleff, P. & Gaston, K.J. (2001) Latitudinal gradients in diversity: real patterns and random models. *Ecography*, **24**, 341–351.
- Krebs, C.J. (1999) *Ecological Methodology*. Addison-Wesley, California.
- Lande, R. (1996) Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos*, **76**, 5–13.
- Lennon, J.J., Koleff, P., Greenwood, J.J.D. & Gaston, K.J. (2001) The geographical structure of British bird distributions: diversity, spatial turnover and scale. *Journal of Animal Ecology*, **70**, 966–979.
- Loreau, M. (2000) Are communities saturated? On the relationship between α , β and γ diversity. *Ecology Letters*, **3**, 73–76.
- MacArthur, R.H. (1965) Patterns in species diversity. *Biological Reviews*, **40**, 510–533.
- Magurran, A.E. (1988) *Ecological Diversity and its Measurement*. Croom-Helm, London.
- Mourelle, C. & Ezcurra, E. (1997) Differentiation diversity of Argentine cacti and its relationship to environmental factors. *Journal of Vegetation Science*, **8**, 547–558.
- Murray, R., Holling, M., Dott, H.E.M. & Vandome, P. (1998) *The Breeding Birds of South-East Scotland: a Tetrads Atlas 1988–94*. The Scottish Ornithologists' Club, Edinburgh.
- Pharo, E.J., Beattie, A.J. & Binns, D. (1999) Vascular plant diversity as a surrogate for bryophyte and lichen diversity. *Conservation Biology*, **13**, 282–292.
- Pielou, E.C. (1984) *The Interpretation of Ecological Data*. Wiley Interscience, New York.
- Poynton, J.C. & Boycott, R.C. (1996) Species turnover between Afrotropical and eastern African lowland faunas: patterns shown by amphibians. *Journal of Biogeography*, **23**, 669–680.
- Price, A.R.G., Keeling, M.J. & O'Callaghan, C.J. (1999) Ocean-scale patterns of 'biodiversity' of Atlantic asteroids determined from taxonomic distinctness and other measures. *Biology Journal of the Linnean Society*, **66**, 187–203.
- Routledge, R.D. (1977) On Whittaker's components of diversity. *Ecology*, **58**, 1120–1127.
- Routledge, R.D. (1984) Estimating ecological components of biodiversity. *Oikos*, **42**, 23–29.
- Ruggiero, A., Lawton, J.H. & Blackburn, T.M. (1998) The geographic ranges of mammalian species in South America: spatial patterns in environmental resistance and anisotropy. *Journal of Biogeography*, **25**, 1093–1103.
- Shmida, A. & Wilson, M.V. (1985) Biological determinants of species diversity. *Journal of Biogeography*, **12**, 1–20.
- Simpson, G.G. (1943) Mammals and the nature of continents. *American Journal of Science*, **241**, 1–31.
- Sørensen, T.A. (1948) A method of establishing groups of equal amplitude in plant sociology based on similarity of species content, and its application to analyses of the vegetation on Danish commons. *Kongelige Danske Videnskabernes Selskabs Biologiske Skrifter*, **5**, 1–34.
- Southwood, T.R.E. & Henderson, P.A. (2000) *Ecological Methods*. Blackwell Science, Oxford.
- Veech, J.A., Summerville, K.S., Crist, T.O. & Gering, J.C. (2002) The additive partitioning of species diversity: recent revival of an old idea. *Oikos*, **99**, 3–9.
- Weihner, E. & Boylen, C.W. (1994) Patterns and prediction of α and β diversity of aquatic plants in Adirondack (New York) lakes. *Canadian Journal of Botany*, **72**, 1797–1804.
- Whittaker, R.H. (1960) Vegetation of the Siskiyou mountains, Oregon and California. *Ecological Monographs*, **30**, 279–338.
- Whittaker, R.H. (1972) Evolution and measurement of species diversity. *Taxon*, **21**, 213–251.
- Whittaker, R.H. (1975) *Communities and Ecosystems*. Macmillan, New York.
- Whittaker, R.H. (1977) Evolution of species diversity in land communities. *Evolutionary Biology*, **10**, 1–67.
- Williams, P.H. (1996a) Mapping variations in the strength and breadth of biogeographic transition zones using species turnover. *Proceedings of the Royal Society, London B*, **263**, 579–588.
- Williams, P.H. (1996b) *WORLDMAP 4 WINDOWS: software and help document 4.1*. Privately distributed (<http://www.nhm.ac.uk/science/projects/worldmap/>), London.
- Williams, P.H., de Klerk, H.M. & Crowe, T.M. (1999) Interpreting biogeographical boundaries among Afrotropical birds: spatial patterns in richness gradients and species replacement. *Journal of Biogeography*, **26**, 459–474.
- Willig, M.R. & Gannon, M.R. (1997) Gradients of species density and turnover in marsupials: a hemispheric perspective. *Journal of Mammalogy*, **78**, 756–765.
- Willig, M.R. & Sandlin, E.A. (1992) Gradients of species density and species turnover in New World bats: a comparison of quadrat and band methodologies. *Latin American Mammalogy: history, biodiversity and conservation* (eds M.A. Mares & D.J. Schmidly), pp. 81–96. University of Oklahoma Press, Oklahoma.
- Wilson, M.V. & Shmida, A. (1984) Measuring beta diversity with presence-absence data. *Journal of Ecology*, **72**, 1055–1064.
- Wolda, H. (1981) Similarity indices, sample size and diversity. *Oecologia*, **50**, 296–302.

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AppendixDERIVATION OF β_z

To obtain an estimate of β_z (z of the power law SAR) in terms of the matching components a , b and c , for two adjacent quadrats, we first write the expected species richness of a smaller quadrat (focal or neighbouring) in terms of this power law:

$$E(s) = kA^z$$

where s is the richness and A is the area of the smaller quadrat. The expected richness, $E(S)$ of the larger quadrat (encompassing the two smaller quadrats) according to the power law SAR is:

$$E(S) = k(2A)^z = 2^z kA^z$$

where k is a constant. The ratio of the larger to smaller quadrat richness depends only on the ratio of larger to smaller quadrat size and z :

$$E(S)/E(s) = 2^z$$

We estimate the richness of a smaller quadrat as the mean of the focal and neighbouring quadrat richness:

$$E(s) = (\alpha_1 + \alpha_2)/2 = (2a + b + c)/2$$

and that of the larger quadrat its observed richness:

$$E(S) = a + b + c$$

Again taking the ratio we obtain the relationship:

$$2^z = 2(a + b + c)/(2a + b + c)$$

Taking logarithms of both sides:

$$z \log(2) = \log(2) + \log((a + b + c)/(2a + b + c))$$

and rearranging we obtain an expression for β_z :

$$z = 1 - \frac{\log((2a + b + c)/(a + b + c))}{\log 2}$$