Maximising phylogenetic diversity in the selection of networks of conservation areas

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Abstract

Phylogenetic diversity (PD) is a biodiversity measure that takes account of phylogenetic relationships (hence evolutionary history) between taxa. It may therefore provide a better currency for conservation evaluation than taxonomic richness. Here, we demonstrate that, contrary to recent assertions, optimisation tools can be used to maximise PD in the context of complementary reserve selection, and that the spatial overlap between sets of sites maximising genus diversity and PD cannot be used as evidence that the first measure is a good surrogate for the second. Nevertheless, in our own analyses using data on bird genera in northwest South Africa we found that near equally effective results are obtained in the selection of complementary sets of sites when maximising for each of these two measures of biodiversity. © 2002 Elsevier Science Ltd. All rights reserved.

1. Introduction

The most effective way of preserving biodiversity is by maintaining self-sustaining populations of native species in their natural ecosystems. This often requires the designation of "nature reserves", areas where conservation of biodiversity is a priority over other forms of land use. However, because maintaining the integrity of these areas often imposes restrictions to other economically and/or socially important human activities, there will always be limitations to the total amount of land that can be set aside for conservation purposes (Vane-Wright et al., 1991).

Methods for the selection of reserve networks based on the complementarity principle (Vane-Wright et al., 1991) have been proposed as a response to these concerns. They look for sets of sites which are highly complementary, in order to improve the efficiency of reserve selection (Pressey and Nicholls, 1989) by maximising the overall amount of biodiversity that can be preserved with the existing limited resources. Most commonly, published studies applying these methods aim at maximising species diversity as a surrogate for the broader biological diversity that ought to be protected (e.g. Williams et al., 1996; Howard et al., 1998; Rodrigues et al., 2000a). However, species richness may not be an ideal measure of biodiversity, as it assumes that all species have *a priori* the same value as conservation units (May, 1990; Vane-Wright et al., 1991; Faith, 1992). Indeed, the extinction of species not closely related to any other living ones (such as the tuataras and the *Welwitshia*) would represent a disproportionate loss of evolutionary history and genetic diversity, much greater than the extinction of other individual species which have many close relatives (such as species of grass snake and *Taraxacum*; May, 1990; Vane-Wright et al., 1991). Those taxonomically distinct species, and the places where they occur, should therefore be given priority in the allocation of conservation resources. This can be achieved if, instead of species richness, a currency of biological diversity which takes the phylogenetic relationship between species (hence evolutionary history) into account (taxonomic distinctness, May, 1990; Humphries et al., 1991; Vane-Wright et al., 1991; phylogenetic diversity, Faith, 1992, 1994; Polasky et al., 2001; or character diversity, Williams et al., 1994;

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Hacker et al., 1998) is maximised in the selection of networks of reserves.

Unfortunately, data on the phylogenetic relationships between species are often scarce and very incomplete, hindering the possibility of their widespread application to reserve planning (Polasky et al., 2001). In this case, it is pertinent to ask if the results of analyses using such data where they are available are significantly different from those obtained using simple species richness (see also Williams and Humphries, 1996).

In a recent issue of *Biological Conservation*, Polasky et al. (2001) have used data on the distribution of 167 bird genera in North America, for which the phylogenetic tree was known, to address this question. Phylogenetic relationships between genera, rather than species, were used because interspecific distances within genera were not available for most species. Their purpose was therefore to determine if generic diversity is an adequate surrogate of phylogenetic diversity (PD). They measured the PD of a given set of genera as the branch length of the phylogenetic tree that includes only those genera. Using heuristic iterative algorithms, they found a set of sites that maximises PD and a set that maximises genus diversity. The use of optimisation algorithms to solve the same problems was rejected because of concern about computational difficulties. The study found that the sets of sites obtained when maximum genus richness or maximum PD were represented followed a very similar spatial pattern, and that the pattern of increase of the two measures of diversity with increasing number of sites was also similar. Based on these two observations, the authors concluded that taxonomic richness is likely to be a good proxy for phylogenetic diversity for the purpose of choosing reserve sites.

The present study has three purposes:

1. To challenge the notions that optimisation tools are too complex, that they cannot be used for solving this type of reserve selection problem, and

that heuristic algorithms provide nearly as good results (a widespread belief after the papers by Csuti et al., 1997; Pressey et al., 1996, 1997).

2. To demonstrate that the interpretation of their results made by Polasky et al. (2001) is partially incorrect, in that the spatial overlap between the sets of sites obtained when maximising genus diversity and PD cannot be used as evidence that the first measure is a good surrogate for the second.

3. To report the results of a new analysis addressing the question of whether taxonomic diversity (here, genus diversity) is a good surrogate for phylogenetic diversity in the selection of complementary networks of priority areas for conservation.

2. How to maximise phylogenetic diversity—an illustrative example

2.1. Measuring phylogenetic diversity

Consider the phylogenetic tree for six hypothetical genera (g1–g6) represented in Fig. 1a. The phylogenetic diversity (PD) of a group of taxa has been defined as the branch length of the phylogenetic tree which includes only those taxa (Faith, 1994; Polasky et al., 2001; Fig. 1b). It is not clear in this definition what happens to basal branches that are common to all the taxa considered. In the original definition of PD (Faith, 1992) and in several subsequent studies (e.g. Faith, 1994; Williams and Humphries, 1994; Williams et al., 1994; Polasky et al., 2001) the option followed was not to consider them in the calculation of PD (Fig. 1c; PD defined as the length of the minimum spanning path). Here, we decided to include them (Fig. 1d,e), which confers important advantages (see later). The rationale for this decision was that each branch in the phylogenetic tree refers to the accumulation of features or characters over a given evolutionary period; therefore, it is logical to consider as part of the PD of a group of
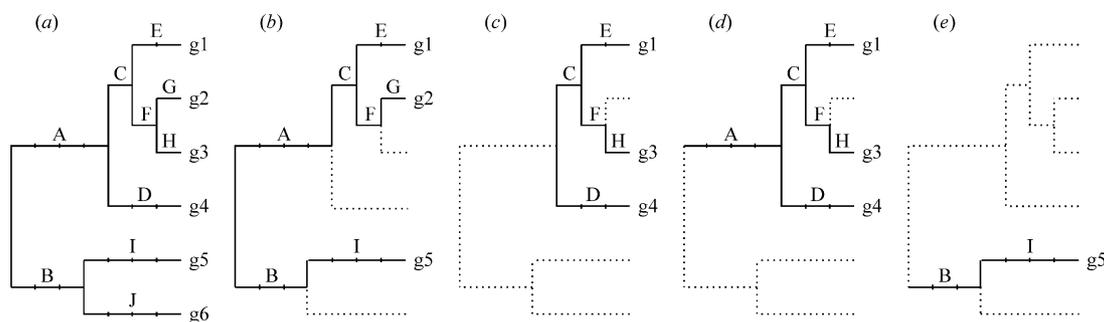
Fig. 1. Phylogenetic tree for six hypothetical genera (g1–g6). The phylogenetic diversity (PD) of a group of taxa is the branch length of the phylogenetic tree which includes only those taxa. The length of each branch (A–J) is given by the number of intervals represented (for example, G has length 1; A has length 4). (a) Tree for all taxa; PD = 24. (b) Sub-tree for taxa g1, g2 and g5; PD = 16. (c) Sub-tree for taxa g1, g3 and g4, excluding the basal branch A; PD = 8. (d) Sub-tree for taxa g1, g3 and g4, including the basal branch A; PD = 12. (e) Sub-tree for taxa g5, including the basal branches; PD = 7. See text for details.

taxa also those features which they have in common, represented by the correspondent basal branches. That is, the amount of evolutionary history accumulated by one particular taxon includes also the fraction of that history that it has in common with its relatives. Otherwise, a set consisting of one genus only (as in Fig. 1e), would have the rather counter-intuitive zero phylogenetic diversity. Note that our purpose here is to measure the PD contained in a set of taxa, not to make comparisons about their relative PD. In our definition of PD, all taxa considered in isolation have the same PD (in this case, PD = 7; Fig. 1e) and therefore all sites containing only one genus are a priori equivalent in terms of conservation priorities. Differences only arise when sets of sites with different generic composition are considered. Including the basal branches in the calculation of PD agrees with the procedure adopted by several previous studies which analysed the amount of PD lost when a given number of taxa goes extinct (e.g. Nee and May, 1997; Heard and Mooers, 2000). In the phylogenetic tree represented in Fig. 1a, for example, the total PD lost when genera g5 and g6 disappear is $B + I + J$. This would be higher than the total PD contained in both genera under the definition that excludes the basal branches. In the measure that includes these branches, the PD lost when a set of genera disappears corresponds to the part of the tree that is unique to those taxa and is always $\leqslant$ their total PD.

A potential problem with this definition of PD is where to draw the limits of the phylogenetic tree, which, in principle, could go back to the origin of life. In practice, it makes no difference if the calculation of PD is based on the tree for only the set of taxa being analysed (say, species within class Aves), or on an expanded tree relating these to other taxonomic groups (say, subphylum Vertebrata, phylum Chordata,...). Expanding the phylogenetic tree would result in a common set of additional branches being added to all taxa. This would increase the values of PD in each cell (the equivalent to the total length of that common set of branches), but not the results of reserve selection, because those branches would be present in all cells. The sensible option in reserve selection is therefore to calculate PD based on a phylogenetic tree of only those taxa that were considered in the analysis.

In practice, the difference between the two ways of measuring PD did not affect the results obtained in this study (see later), and it is most unlikely to affect any result of complementary reserve selection aimed at maximising PD. This is because, in order to maximise PD for any phylogenetic tree, it is necessary to select at least two of the most distinct taxa (i.e. to include the most basal node of the tree; see Nee and May, 1997). In the tree represented in Fig. 1, this would mean selecting at least one genus from g1, g2, g3 and g4, and another one from g5 and g6, requiring the inclusion of branches

A and B regardless of the type of PD measure applied. However, including the basal branches in the phylogenetic tree brings considerable computational advantages for calculating the PD of a set of taxa or of a set of sites (Fig. 2 illustrates how this can be done using simple linear algebra), allowing the use of integer linear programming to obtain optimal solutions to reserve selection problems.

2.2. Maximising phylogenetic diversity in reserve selection

The solution to the problem of obtaining the minimum set such that the maximum PD is represented (equivalent to requiring that all branches are represented) can be obtained by solving the following set covering problem (Underhill, 1994; Rodrigues et al., 2000b):

$$\text{Minimise} \quad \sum_{j=1}^{n} x_j \tag{1}$$

$$\text{Subject to} \quad \sum_{j=1}^{n} a_{ij} x_j \geqslant 1 \qquad i = 1, 2, \ldots, m \tag{2}$$

$$x_j \in \{0, 1\} \qquad j = 1, 2, \ldots, n \tag{3}$$

where n is the number of sites, m is the number of branches, a_{ij} is one if branch i is present in site j and zero otherwise (i corresponds to the rows and j to the columns in matrix $\mathbf{BS_{0/1}}$, Fig. 2), and variable x_j is one if and only if site j is selected. The objective function (1) is to minimise the number of sites selected. Inequalities (2) ensure that each of the m branches must be represented at least once. The integrality restrictions (3) state that each site j is an indivisible unit (Rodrigues et al., 2000b).

The solution to the problem of minimising the number of sites such that all genera are covered is represented in exactly the same way, but now m is the number of genera and a_{ij} is one if genus i is present in site j and zero otherwise (i corresponds to the rows and j to the columns in matrix $\mathbf{GS}$, Fig. 2).

For the data matrices represented in Fig. 2, the optimal solution for both problems is to select sites s3 and s4. It is not a coincidence that the same result is found in both cases. Because the maximum PD (in this case, equal to 24) can only be obtained by representing all of the branches, and because all taxa have one unique branch, the maximum PD is only obtained by having all the genera represented. Consequently, the problem of representing the maximum PD in the minimum number of sites is equivalent to the problem of representing all genera in the minimum number of sites. It would therefore be expected that Polasky et al. (2001) should obtain the same result when prioritising for PD or for the diversity of genera (Fig. 5 in Polasky et al., 2001).

(a)

$\mathbf{BG} =$ (rows A–J, columns g1 g2 g3 g4 g5 g6):

	g1	g2	g3	g4	g5	g6
A	1	1	1	1	0	0
B	0	0	0	0	1	1
C	1	1	1	0	0	0
D	0	0	0	1	0	0
E	1	0	0	0	0	0
F	0	1	1	0	0	0
G	0	1	0	0	0	0
H	0	0	1	0	0	0
I	0	0	0	0	1	0
J	0	0	0	0	0	1

$\mathbf{l} =$ A:4 B:3 C:1 D:3 E:2 F:1 G:1 H:1 I:4 J:4

$\mathbf{GS} =$ (rows g1–g6, columns s1 s2 s3 s4):

	s1	s2	s3	s4
g1	1	1	1	0
g2	1	0	0	1
g3	1	0	0	1
g4	1	0	1	0
g5	0	0	1	0
g6	0	1	0	1

$\mathbf{BS} =$ (rows A–J, columns s1 s2 s3 s4):

	s1	s2	s3	s4
A	4	1	2	2
B	0	1	1	1
C	3	1	1	2
D	1	0	1	0
E	1	1	1	0
F	2	0	0	2
G	1	0	0	1
H	1	0	0	1
I	0	0	1	0
J	0	1	0	1

$\mathbf{BS_{0/1}} =$ (rows A–J, columns s1 s2 s3 s4):

	s1	s2	s3	s4
A	1	1	1	1
B	0	1	1	1
C	1	1	1	0
D	1	0	1	0
E	1	1	1	0
F	1	0	0	1
G	1	0	0	1
H	1	0	0	1
I	0	0	1	0
J	0	1	0	1

(b)

$\mathbf{subBG} =$ (rows A–J, columns g1 g2 g5):

	g1	g2	g5
A	1	1	0
B	0	0	1
C	1	1	0
D	0	0	0
E	1	0	0
F	0	1	0
G	0	1	0
H	0	0	0
I	0	0	1
J	0	0	0

$\mathbf{a} =$ A:2 B:1 C:2 D:0 E:1 F:1 G:1 H:0 I:1 J:0

$\mathbf{a_{0/1}} =$ A:1 B:1 C:1 D:0 E:1 F:1 G:1 H:0 I:1 J:0

$\mathbf{PD} = \mathbf{a_{0/1}}^T \cdot \mathbf{l} = [1\ 1\ 1\ 0\ 1\ 1\ 1\ 0\ 1\ 0] \cdot [4\ 3\ 1\ 3\ 2\ 1\ 1\ 1\ 4\ 4]^T = 16$

(c)

$\mathbf{subBS} =$ (rows A–J, columns s1 s4):

	s1	s4
A	1	1
B	0	1
C	1	0
D	1	0
E	1	0
F	1	1
G	1	1
H	1	1
I	0	0
J	0	1

$\mathbf{b} =$ A:2 B:1 C:1 D:1 E:1 F:2 G:2 H:2 I:0 J:1

$\mathbf{b_{0/1}} =$ A:1 B:1 C:1 D:1 E:1 F:1 G:1 H:1 I:0 J:1

$\mathbf{PD} = \mathbf{b_{0/1}}^T \cdot \mathbf{l} = [1\ 1\ 1\ 1\ 1\ 1\ 1\ 1\ 0\ 1] \cdot [4\ 3\ 1\ 3\ 2\ 1\ 1\ 1\ 4\ 4]^T = 20$

Fig. 2. Measuring phylogenetic distance (PD) for a data set. (*a*) Data matrices for the phylogenetic tree represented in Fig. 1*a*. Matrix **BG** corresponds to the distribution of branches (A–J) in each genus (g1–g6). Vector **l** corresponds to the length of each branch. Together, **BG** and **l** have all the information of the phylogenetic tree represented in Fig. 1*a*. Matrix **GS** represents the distribution of each genus in each of four sites considered (s1–s4). The product of matrix **BG** (dimensions 10×6) by matrix **GS** (6×4) results in matrix **BS** (10×4), which indicates the number of times each branch is represented in each site. Converting this to a 0/1 matrix, matrix **BS$_{0/1}$** is obtained, providing the distribution of each branch in each site. (*b*) Computation of PD for a set of genera. Matrix **subBG** corresponds to a submatrix of **BG** considering only genera g1, g2 and g5 (as in Fig. 1*b*). Vector **a** is the sum of the columns of **subBG**; converted into the 0/1 $\mathbf{a_{0/1}}$ vector, this indicates which branches are present in the tree which includes only these genera (Fig. 1*b*). PD for the three genera is then given by the multiplication of the transposed vector $\mathbf{a_{0/1}^T}$ by the vector **l**. (*c*) Computation of PD for a set of sites. Matrix **subBS** corresponds to a submatrix of **BS** considering only sites s1 and s4. Vector **b** is the sum of the columns of **subBS**, subsequently converted into the 0/1 $\mathbf{b_{0/1}}$ vector. PD for the two sites is then given by the multiplication of the transposed vector $\mathbf{b_{0/1}^T}$ by the vector **l**. This is equivalent to calculating the PD for the taxa present in sites s1 and s2 (all genera except g5). This way of measuring PD can be applied if, instead of a phylogenetic tree, the relationships between taxa are represented by a cladogram of features or characters (e.g. Faith, 1992; Williams and Humphries, 1996). In that case, matrix **BG** would represent the distribution of features/characters in each taxon, and vector **l** would be a column of 1s (unless different characters were given different weights).

What may be surprising is that Polasky et al. (2001) did not obtain *exactly* the same results to the problems of obtaining the minimum sets that maximise PD or cover all genera. There are two explanations. First, most set-covering problems have a diversity of equally optimal solutions (see later). The results presented in the two maps in Fig. 5 of Polasky et al. (2001), presented as solutions, respectively, to each of the two problems, are therefore two of the possible solutions to the same problem. Second, the problems were not solved optimally, and this, as the authors acknowledge, explains why sets of different sizes were found (15 areas in one case, 16 in the other). The use of sub-optimal algorithms has been justified by arguing that "optimisation algorithms can present computational difficulties" and that "in particular, it is difficult to solve optimisation algorithms

when the objective is to maximise a diversity measure based on the branch lengths of the phylogenetic tree for species represented in the set of chosen sites'' (Polaski et al., 2001). Here, we have demonstrated that the problem of representing the maximum PD is also a set-covering problem, and that it can be solved as easily as the problem of representing maximum taxonomic richness.

Finding that the solutions to the problems of representing the maximum PD and all genera are similar or identical is not sufficient evidence that taxon diversity is a good surrogate for PD. What needs to be investigated is what happens when there are limited resources and not all genera can be represented. The analysis in Fig. 5 of Polasky et al. (2001) indicates little agreement in the order in which sites were selected in each case. However, more important than establishing if the geographical location of the sites is the same, is to assess how well sets of sites selected to maximise genus richness perform in terms of representing PD, when it is not possible to select a sufficient number of sites to represent all genera or the maximum PD. In Polasky et al. (2001), this corresponds to comparing the curves for the accumulation of PD when prioritising for genus diversity (Fig. 3) and when prioritising for PD (Fig. 2). The similarity of these two curves is the best indication given in this study that generic diversity performs quite well in representing PD.

The problem of maximising the PD in a given set of sites can be formulated as the maximal covering location problem (MCLP, Church et. al., 1996):

$$\text{Maximise} \quad \sum_{i=1}^{m} l_i y_i \tag{4}$$

Subject to

$$\sum_{j=1}^{n} a_{ij} x_j \geqslant y_i, \qquad i = 1, 2, \ldots, m \tag{5}$$

$$\sum_{j=1}^{n} x_j \leqslant k, \tag{6}$$

$$x_j \in \{0, 1\} \qquad j = 1, 2, \ldots, n \tag{3}$$

$$y_i = \in \{0, 1\} \qquad i = 1, 2, \ldots, m \tag{7}$$

where l_i is the length of branch i, y_i is one if branch i is covered and zero otherwise, k is the maximum number of sites that can be represented and all the other variables are as before.

The objective function (4) maximises the total PD (sum of the length of all branches represented). Each one of the restrictions (5) indicates that the branch i cannot be counted as preserved if none of the sites where it exists is selected. Restriction (6) ensures that the total number of sites does not exceed k. Restrictions (3) and (7) state that both sites and branches are indivisible units.

The problem of representing the maximum number of genera in k sites can be formulated in an equivalent way, but replacing the objective function by:

$$\text{Maximise} \quad \sum_{i=1}^{m} y_i \tag{8}$$

where y_i refers to genus i; a_{ij} (in restrictions 5) is now one if genus i is present in site j and zero otherwise.

These two problems represent two different ways of maximising biodiversity in a given set of sites: in the first, the unit of biodiversity is one unit of branch length, each one considered to have the same value; in the second one, the biodiversity units are the number of genera, all genera considered to be of equal value.

Unlike the set-covering problem, there is no reason why the results for these two MCLP should be the same (for k less than the minimum number of sites needed to represent all genera or all branches). For example, for
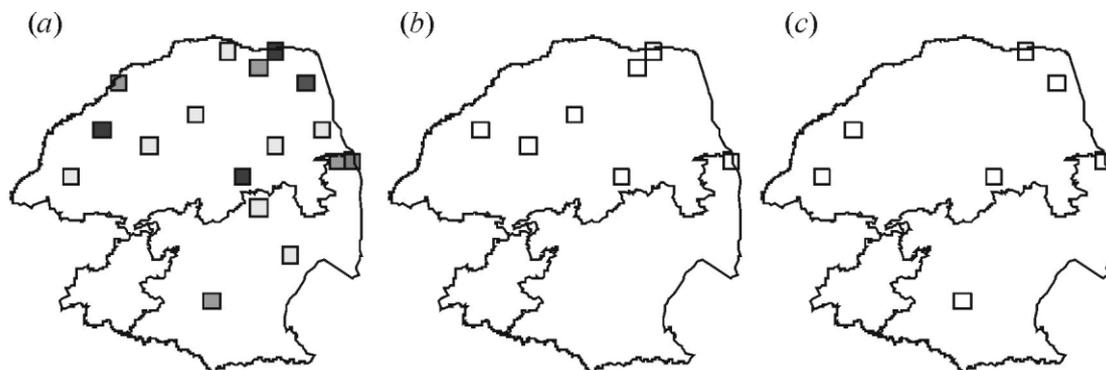
Fig. 3. Spatial location of optimal solutions obtained to the problem of finding the minimum number of sites which represents all genera or maximum phylogenetic diversity of birds in the study area (Northern Province, top; Gauteng, bottom left; and Mpumalanga, bottom right). (a) Overlap between the 10 solutions obtained; darker cells correspond to those sites that have been selected more frequently (i.e. in more minimum sets). (b, c) Two of the optimal solutions found.

the data represented in Fig. 2, the results of maximising PD in one site (site s3; PD = 17, No. of genera = 3) are different from those of maximising number of genera (site s1; No. of genera = 4, PD = 13). It may therefore happen that, for limited resources, maximising taxon diversity does not provide an adequate surrogate for maximising PD. We used a data set on the distribution of birds in South Africa to explore this further. These data are used here as an exemplary set and, therefore, these results should not be interpreted as an attempt to propose a new reserve network in South Africa.

3. Application to the birds of South Africa

The Southern African Bird Atlas Project (SABAP; Harrison et al., 1997) has provided the most comprehensive information currently available on the distribution of birds in southern Africa. Data were mainly collected between 1987 and 1992, at a spatial resolution of a quarter-degree grid for Lesotho, Namibia, South Africa, Swaziland and Zimbabwe, and on a half-degree grid for Botswana (for a detailed description of the methods used in the SABAP, see Harrison et al., 1997). In this study, we used the presence/absence data for 166 genera in the South African provinces of Gauteng, Mpumalanga and Northern Province (319 quarter-degree grid cells). As in Polasky et al. (2001), we used data on the phylogenetic relationships between genera, rather than species, because data on the interspecific distances within each genus were not available for most species. The taxonomy of each genus followed Sibley and Monroe (1990) and was not always coincident with the one used in Harrison et al. (1997).

As in Polasky et al. (2001), the phylogenetic relationships between genera were obtained from the phylogenetic tree published by Sibley and Ahlquist (1990, pp. 838–870), who obtained phylogenetic distances between genera by average linkage (UPGMA) clustering of DNA-DNA hybridisation distances ($\Delta T_{50}H$). The phylogenetic tree for our data set had 326 branches and a total PD = 1582.1 $\Delta T_{50}H$. The 166 genera analysed covered 73% of the total of 589 species found in the study area.

The minimum set found to be needed to represent all genera or maximum PD had seven sites. This problem had several optimal solutions, and 10 of these (selected randomly and without replacement from the set of optimal solutions—see Rodrigues et al., 2000b; Gaston et al., 2001) were obtained. By mapping them (Fig. 3), we found that some particular sites tend to be selected more often (Fig. 3a) but that different solutions may look quite distinct in terms of the spatial location of particular sites (Fig. 3b,c).

Solving the corresponding MCLPs, sets of sites were obtained which represent the maximum number of genera or the maximum PD within a number of sites $k \leqslant 7$. Most of these problems had more than one equally optimal solution. In that case, 10 solutions or the total number of existing ones, if $\leqslant 10$, were obtained. The average PD and average number of genera across all replicates were calculated in each case.

We found that the solutions obtained by maximising the number of genera represented in a given set of sites $k \leqslant 7$ are very similar to the ones obtained by maximising the PD in the same number of sites (Table 1). More specifically, we found that when maximising for PD, the optimal solutions obtained were always optimal solutions to the problem of maximising the number of genera in the same number of sites. And that when maximising for number of genera, some of the optimal solutions found were also optimal solutions to the problem of maximising PD or else they had a value of PD very close to the one obtained by maximising PD in the same number of sites.

For comparative purposes, we also obtained near-minimum sets representing all genera and maximum PD using the greedy heuristic algorithms described by Polasky et al. (2001). The near-minimum number of sites needed to represent all genera was eight and the

Table 1
Results of maximal covering location problems (MCLP) maximising the number of genera and maximising the phylogenetic diversity (PD) that can be represented in a given number of sites (between one and seven)[a]

No. of sites	Maximise for No. genera			Maximise for PD		
	Average No. genera	Average PD	No. of solutions	Average No. genera	Average PD	No. of solutions
1	142	1413.6	1	142	1413.6	1
2	158	1541.25	2	158	1542.5	1
3	161	1555.82	6	161	1558.4	2
4	163	1568.6	⩾10	163	1568.6	⩾10
5	164	1571.3	⩾10	164	1575.4	⩾10
6	165	1577.26	⩾10	165	1579.4	⩾10
7	166	1582.1	⩾10	166	1582.1	⩾10

[a] For each problem, the average number of genera, the average PD and the number of optimal solutions found are presented.

near-minimum number of sites needed to represent maximum PD was nine. These correspond to an extra cost of 14 and 29% in relation to the minimum set of seven sites.

As expected, these results have not been affected by the measure of PD applied, as the first site selected in any case (both in the optimisation and the heuristic approaches) was one which included the basal branches of the phylogenetic tree (i.e. a site which had members of both the Eoaves and Neoaves Infraclasses).

4. Discussion

This study illustrates how reserve selection problems aiming at maximising phylogenetic diversity can be formally represented and solved optimally as integer linear programming problems. Using the C-Plex software (ILOG, 1999) on a Pentium II PC (128 MB RAM), all the problems presented in this analysis were solved in less than 3 s. Indeed, our experience in previous studies using other data sets indicates that large set-covering problems can be solved very quickly (e.g. the problem of finding the minimum set representing 651 bird species in 1858 grid cells in South Africa is solved in 2.2 s). On the other hand, using greedy heuristic algorithms gives no guarantee that an optimal solution can be obtained. Although the one or two additional sites selected in the present case may seem negligible in terms of the efficiency of the algorithms, the additional 14 and 29% costs in reserve acquisition would be highly significant if this was an application to a real life problem with a limited budget. This illustrates the point that, contrary to widespread belief (e.g. Pressey et al., 1996, 1997; Csuti et al., 1997; Howard et al., 1998; Williams, 1998; Polasky et al., 2001), these heuristic approaches do not necessarily provide solutions which are optimal or only slightly sub-optimal (see also Rodrigues et al., 2000b).

Perhaps more important than the optimality of the solution obtained, the main advantage of using optimisation tools is the flexibility of situations that can be represented and solved as linear integer programming problems (Rodrigues et al., 2000b). As measured in this study, PD is just another possible currency of biodiversity, which (as long as the phylogenetic data are available) can easily be integrated in a diversity of problems and situations. For example, an MCLP problem aiming at maximising PD in k sites, may be subjected to a diversity of additional restrictions, such as: that at least 25% of those k sites selected need to be owned by the State; that a given species i needs to be reserved in at least 50% of its range; or that the set of sites selected must have a human population $< 1,000,000$. The possibilities are numerous, and can be solved exactly if stated as integer problems. However, it would not be obvious how to formulate an "intuitive" heuristic which could satisfactorily solve these more complex problems.

Complementarity-based reserve selection problems typically have several optimal solutions (Table 1; e.g. Arthur et al., 1997; Csuti et al., 1997; Williams et al., 2000; Gaston et al., 2001), and these may look quite distinct in terms of the spatial position of individual sites (Fig. 3). This is why the comparison between results to the problems of maximising PD or the number of genera cannot rely on the spatial overlap between solutions (as in Polasky et al., 2001) and should instead be made in terms of their relative performance in diversity (PD or genera) representation (Table 1). This is also true of other comparative reserve selection analyses, and studies which based their conclusions on the analysis of spatial overlap between solutions may need revision (e.g. Lombard, 1995; Freitag and van Jaarsveld, 1998; van Jaarsveld et al., 1998; Erasmus et al., 1999; see Reyers and van Jaarsveld, 2000 for such a revision).

When evaluated in terms of the effectiveness in maximising the PD of those areas selected to maximise generic richness (Table 1), the results for birds in South Africa support the assertion by Polasky et al. (2001) that taxon diversity may be a good surrogate for phylogenetic diversity. This is likely to be the result of a highly significant positive relationship between the values of both measures of diversity in each site (Fig. 4), a result which agrees with previous findings (Williams and Humphries, 1996; Hacker et al., 1998).

We believe that it is likely that these findings can be generalised, and that, in practice, taxonomic richness (usually, species richness) can continue to be safely used as a surrogate for phylogenetic diversity within the same taxonomic group. However, it may be instructive to consider those situations in which this may not be the case: if the phylogenetic tree is highly unbalanced, with some of the branches being very ramified while others correspond to monophyletic taxa, *and* if there is a spatial segregation between the sites where these two types of branches occur. In this case, it is possible that reserve selection based on taxonomic richness tends to select sites with many closely related species while selection
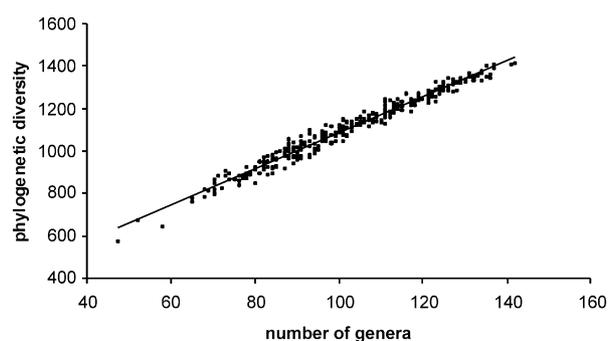
Fig. 4. Relationship between the number of genera and the phylogenetic diversity in each cell ($r^2 = 0.97$; $n = 319$; $P < 0.0001$).

based on PD will tend to select sites with monophyletic taxa. This is what happens in the example represented in Figs. 1 and 2: site s1 is the richest in taxa, but its four genera are taxonomically close; site s2 has only two genera, but these are taxonomically quite distinct, and therefore s2 has higher PD than s1 (14 instead of 13). In this example, the relationship between number of genera and PD at each site is not only very weak ($R^2 = 0.057$, P-value $= 0.76$) but it actually has also a negative slope ($b = -0.5$). A parallel situation may occur in practice if the study area includes sites with very marked differences in taxonomic structure (Gaston, 2000). Insular biotas, for example, such as isolated islands and lakes, may have suffered evolutionary radiations which resulted in the separate evolution of particular branches of the phylogenetic tree, for example, the radiation of lemurs in Madagascar. It may also be the case with the bumble bees of the sibiricus-group used in WORLD-MAP (2000), which have a higher species richness in South America and a higher PD in Asia. This effect is likely to be more noticeable at the species, rather than at the generic, level.

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