

# Phylogenetic diversity: a quantitative framework for measurement of priority and achievement in biodiversity conservation

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The value of biodiversity lies in its option value for the future, the greater the complement of contemporary biodiversity conserved today, the greater the possibilities for future biodiversity because of the diverse genetic resource needed to ensure continued evolution in a changing and uncertain world. From this perspective, biodiversity option value can be equated with richness in the different features expressed by species. An individual species of greater value is one contributing more novel features to a given subset. The feature diversity of species and communities is difficult to estimate directly, but can be predicted by the phylogenetic relationships among the species. The 'Phylogenetic Diversity' measure (PD) (Faith, 1992a) estimates the relative feature diversity of any nominated set of species by the sum of the lengths of all those branches spanned by the set. These branch lengths reflect patristic or path-length distances. This study first reviews and expands on some of the properties of PD, and develops simple modifications of the measure ( $\Delta$ nPD and  $\epsilon$ nPD) to enable capture of both the phylogenetic relatedness of species and their abundances in each sample. Then the application of PD,  $\Delta$ nPD and  $\epsilon$ nPD to a wide range of conservation and resource management issues is demonstrated using avian case studies. Supertree construction procedures (matrix representation using parsimony analysis; average consensus) were used to combine the extensive DNA–DNA hybridization tree of Sibley & Ahlquist (1990) with numerous, recently published phylogenetic reconstructions to derive a phylogenetic tree for the global avian fauna. Using this supertree as a systematic framework, the utility of PD was demonstrated in four case studies: (i) state of the environment reporting, with changes in avian faunas resulting from extinctions quantified as indicators of the *state of biodiversity* at Global, New Zealand and Waikato region scales, and changes in available habitat quantified as indicators of *pressures on biodiversity* in the Waikato region; (ii) setting priorities for threatened species management, with PD as a measure of option value integrated with information on survivorship expectations to develop a ranking among threatened New Zealand forest bird species; (iii) monitoring biotic response to management, with data from 5-minute counts used to analyse changes in forest bird communities under three management regimes in New Zealand; and (iv) selection of indicator species, with PD used to objectively identify subsets of species in the Global, New Zealand and Waikato avian faunas that comprise a high proportion of the option value in those faunas. © 2002 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2002, 76, 165–194.

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## INTRODUCTION

Conservation and resource management agencies around the world face hard choices about where and how to conserve biodiversity with limited financial resources. If such choices are to be made in an informed way, there is a need for robust, quantitative methods of measurement and valuing biodiversity.

IUCN (1980) interpreted the value of biodiversity as lying in its option value for the future—the greater the complement of contemporary biodiversity we are able to conserve today, the greater the possibilities for future biodiversity because of the diverse genetic resource needed to ensure continued evolution in a changing and uncertain world. From this perspective, biodiversity option value can be equated with species richness, plus the richness of activities each species undergoes during its existence through events in the life of its members, plus the non-phenotypic expression of its genome (Erwin, 1991). Thus, option value is

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associated with richness in the different features expressed by organisms (Faith, 1992a,b; Weitzman, 1992; Williams & Humphries, 1996). An individual species of greater value is one contributing more novel features to a given subset. For example, a pit-making weevil (*Psepholax coronatus* Broun) and a platypus weevil (*Platypus apicalis* White) (both in the beetle family Curculionidae) represent fewer features in total, and so less option value in the New Zealand *Nothofagus* tree borer guild, than the combination of a jewel beetle (*Nascioides enysi* (Sharp), family Buprestidae) and a platypus weevil. Features (phenotypic characters or the genes that code them) can thus provide a 'currency' of biodiversity value.

Resource managers needing to estimate richness of features usually are unable to measure this directly, or at best are able to do so only for a small sample of genes or characters. Because a 'complete' set of all features for a set of species will never be observed directly, inference of relative contributions of different species to overall feature-diversity will have to be made using some surrogate. Quantifying biodiversity at the feature level is therefore an estimation problem. However, because genes and characters are inherited, the relative feature richness and thus biodiversity value of different species in communities can be estimated readily using knowledge of genealogical relationships among the species that make up those communities. Phylogenetic Diversity (PD) (or Feature Diversity) was first proposed by Faith (1992a) as a measure of biodiversity option value. PD simply measures how much of the pattern of feature diversity – how much of the branching pattern in the phylogenetic tree – is represented in a sample of species. A species then contributes novel features, and contributes option value, if it represents a thus-far unrepresented part of the evolutionary history of the group.

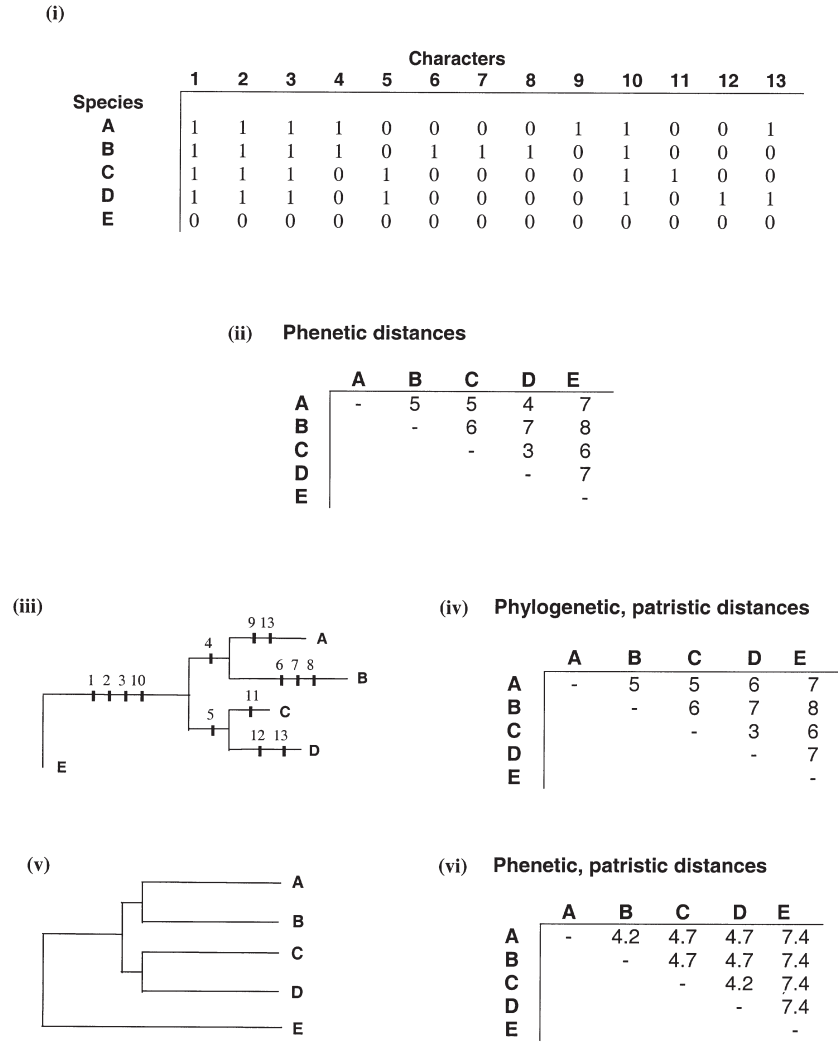
The application of PD to the problem of reserve selection has been demonstrated by Faith (1992a) and Moritz & Faith (1998), but the applicability to the greater range of conservation and resource management issues has to date not been adequately demonstrated. As pointed out by Clarke & Warwick (1998), to date there has been little carry over of PD, and related taxonomic measures (e.g. Vane-Wright, Humphries & Williams, 1991; Crozier, 1992; Crozier & Kusmierski, 1994; Humphries *et al.*, 1995; Izsák & Papp, 2000; and references therein), into the area of environmental monitoring and assessment, where the emphasis is not on choosing species to conserve, but instead on monitoring for environmental degradation or the benefits of remediation. Clarke & Warwick (1998) considered that the lack of uptake was related to differences in data requirements: the general utility of simple species inventories for assessment of conservation status, in contrast to the need for

community samples with recorded abundances for an assessment changes in assemblages through time or in space. A further contributory factor is the general lack of understanding of phylogenetics among ecologists and resource managers, a point accentuated by the proliferation, without consensus, of biodiversity measures that employ phylogeny to weight species (references above) and the instability in phylogenetic hypotheses for particular taxonomic groups.

In this paper, first I recapitulate and expand on some of the properties of PD. Next, I develop simple modifications of the index (here termed  $\Delta$ nPD and  $\epsilon$ nPD) to enable capture of both the phylogenetic relatedness of species and their abundances in each sample. Finally, I demonstrate the application of PD,  $\Delta$ nPD and  $\epsilon$ nPD to a wide range of conservation issues using avian case studies.

### CALCULATING PD FOR COMMUNITIES

Phylogenetic analysis is an approach to evolutionary reconstruction that groups taxa in such a way that those with historically more-recent ancestors form groups nested within groups of taxa with more-distant ancestors. This nesting can be represented as a branching tree diagram or cladogram, which is a hypothesis of the evolutionary history of the taxa. This analysis is usually performed by searching for nested groups of shared derived states (features) in an array of characters. When a character changes from an ancestral state to a derived state in a lineage it is unique historically, and it will be passed on to all of the descendants of that lineage (even if the character is later modified into something else). Therefore, the branching sequence of evolution can be deduced by searching for nested groups of shared derived character states (synapomorphies) among the taxa being analysed. So, if a derived character state is observed in two or more taxa, then we can hypothesize that they share this apomorphy because they are descended from a common ancestor, and that they inherited the apomorphy from the ancestor. Thus, phylogenetic analysis is simply the search for nested sets (a hierarchy) of synapomorphies among the taxa. Each synapomorphy represents contemporary evidence for a prior evolutionary event. Furthermore, not only does phylogenetic analysis inform about the branching pattern in evolution, it also provides estimates of the relative amounts of change or path-length in different branches. For any phylogenetic estimation, the relative branch length is assumed to predict the relative number of novel features that have arisen in a given line of descent (Faith, 1992b) (Fig. 1). The phylogenetic pattern for the taxonomic group in question therefore provides a prediction of underlying feature-diversity patterns; a subset of taxa that spans



**Figure 1.** Estimating feature diversity from phenetic and phylogenetic distances. (i) A simple hypothetical data matrix for states (0 = absence, 1 = presence) in 13 characters in each of five species. Each unique state for a character represents a feature. (ii) Matrix of phenetic distances among species pairs corresponding to a simple count of the number of feature differences between pairs of species. (iii) A cladogram depicting the most parsimonious reconstruction of the phylogeny of Species A–E, based on cladistic principles (analysis implemented with PAUP; Swofford, 1998) which makes use of the direction of evolutionary change of character states (for each character, state 0 is assumed to be ancestral to state 1) and recognizes that when a character changes from an ancestral state to a derived state in a lineage it is historically unique, and it will be passed on to all of the descendants of that lineage (even if the character is latter modified into something else). The branch lengths are scaled in proportion to the number of characters that changed from state 0 to state 1 (i.e. proportional to feature richness). The characters involved are indicated on each branch. In the phylogeny corresponding to the most parsimonious tree, Species E is identified as basal in possessing no uniquely derived (apomorphous) character states. Species A and B form a clade distinguished by a shared apomorphous state for character 4, and Species C and D form a clade distinguished by a shared apomorphous state for character 5. The share derived state in character 13 in Species A and D is recognized as a case of convergent, independent evolution. (iv) Matrix of estimated (patristic) phylogenetic distances among species pairs corresponding to the analysis presented in (iii). (v) A phenogram based on phenetic dissimilarity, using the Russell and Rao coefficient of association and unweighted pair-group arithmetic average linkage (UPGMA) clustering. In phenetic analysis the interest is in number of matched states in characters (e.g. shared occurrence of state 1 within each character), and not directionality of state changes (e.g. changes from state 0 to state 1). (vi) Matrix of estimated (patristic) phenetic distances among species pairs corresponding to the analysis presented in (v).

a greater portion of the tree consequently is more diverse in this sense. Estimates of branch lengths in phylogenetic trees can be made from many different types of data – such as morphological characters, DNA sequences, RAPD-fingerprinting, DNA–DNA hybridization, DNA secondary structures, allozymes – and from different ordination algorithms.

Faith (1992a) defined PD of any subset of species<sup>1</sup>,  $Q$ , from a species pool  $T$ , as equal to the sum of the lengths of all those branches that are members of the minimum spanning path defined by  $Q$  in the cladogram depicting relationships among all species in  $T$ .

In many cases, the simplicity of PD means that it can be calculated directly from the cladogram, by adding together the appropriate branch lengths, for the given subset of species,  $Q$ . For large cladograms, or for repeated calculations of PD for many different subsets of species from the same cladogram, a simple computer-based algorithm is clearly useful. As shown by Faith (1992a), the PD of any subset of species ( $PD_Q$ ) can be readily obtained from a summary matrix consisting of pair-wise distances between species, taken from the cladogram. In this matrix, the distance between two species,  $i$  and  $j$ ,  $d_{ij}$ , is the sum of the lengths of the branches on the shortest path between them, and

$PD_Q$  = minimum gain of adding  $k$ , over all  $i, j$  in set  $Q$ , of

$$0.5[d(k, i) + d(k, j) - d(i, j)], \quad (1)$$

In some situations a survey may reveal only one species at a particular site. Under the definition of PD of Faith (1992a), there is no corresponding minimum spanning path between two species in this situation and thus PD must be scored as zero. However, given that branch lengths provide a relative estimate of feature richness associated with each branch within the cladogram, including terminal branches, each species recognized must contribute some level of unique feature diversity. That is, the unique contribution of a species is its ‘pattern complementarity’: the degree to which that species contributes unrepresented features to the set defined by all other species. I here define species-unique feature diversity,  $PD_{SU}$ , as the contribution to tree spanning path length if that species were to be added to the cladogram depicting the phylogenetic relations among all other species in the set  $T$ :

For Species  $k$ ,  $PD_{Su_k}$  = minimum gain of adding  $k$ , over all  $i, j$  in  $T$ , of

$$0.5[d(k, i) + d(k, j) - d(i, j)] \quad (2)$$

<sup>1</sup>For clarity in presentation, I make reference to species throughout. However, PD can be applied to any level of taxonomic resolution.

which is equivalent to

$$PD_{Su_k} = d(k, T \setminus k) \quad (3)$$

and

$$PD_{Su_k} = PD_T - PD_{T \setminus k}, \quad (4)$$

where  $T \setminus k$  is species pool  $T$  exclusive of  $k$ . Given that the information of interest is feature diversity or option value, the feature diversity unique to species  $k$  (i.e.  $PD_{Su_k}$ ) can also be viewed as its information content,  $I_k$ .

The indicator value (IV) of species  $k$  alone is proportional to its contribution to total feature diversity or information content, defined as:

$$IV_k = PD_{Su_k} / PD_T. \quad (5)$$

In many situations we are interested in the information content of species in  $Q$  subset of species pool  $T$ . We can then generalize eqns (2), (3), and (5) to

$$I_k = d(k, Q \setminus k) \quad (6)$$

and generalize eqn (5) to

$$IV_k = d(k, Q \setminus k) / PD_Q. \quad (7)$$

where  $Q \setminus k$  is set  $Q$  exclusive of  $k$ , and  $Q \leq T$ . For many applications,  $I_k$  is simply determined as the minimum distance, in the pairwise distances matrix, between species  $k$  and the other species in  $Q$ .

In most situations we have samples, comprising either species lists (presence/absence data) or estimates of relative abundance of species (compositional data). Let us consider these two cases in turn.

#### PRESENCE/ABSENCE DATA AND CALCULATION OF PD

In our example from Fig. 1, we have a potential species pool  $T$  of five species (Species A–E). In order to illustrate the calculation of PD, let us assume that an inventory at a particular site yields presence/absence data, where Species A, C, D and E are indicated to be present, and Species B is indicated to be absent.

The steps to calculation the PD for this sample are as follows.

##### Step 1.

- Search data to find first two species recorded as present (e.g. Species A, Species C).
- From the distance matrix, obtain the branch length distance between this species pair, e.g.  $d(A, C) = 5$ .
- Then go to Step 2.

Note that if only one species was recorded in the sample, PD would be calculated as  $PD_{SU}$  using eqn (2) [or  $I$  using eqn (6)] and the result outputted to file.

e.g. Species A has  $PD_{SU}$  score of 2, Species B has  $PD_{SU}$  of 3, etc.

*Step 2*

- Calculate gain in adding next species to the set e.g. adding D to set AC.

This gain is calculated using eqn (1), as  $0.5[d(D,A) + d(D,C) - d(A,C)]$ .

Gain in this example is  $0.5 [6 + 3 - 5] = 2$ .

*Step 3*

- Add calculated score from step 1 to that in step 2. e.g.  $5 + 2 = 7$ .

*Step 4*

- Calculate gain in adding next species to the set e.g. adding E to set ACD.

- First calculate the gain of adding E to set AC using  $0.5[d(E,A) + d(E,C) - d(A,C)]$ .

- Then calculate the gain of adding E to set AD using  $0.5[d(E,A) + d(E,D) - d(A,D)]$ .

- And finally calculate the gain of adding E to set CD using  $0.5[d(E,C) + d(E,D) - d(C,D)]$ .

- Take the lower of these three values as being the gain of adding E to set ACD; that is, minimum gain by adding  $k$  over all  $i$  and  $j$  in set  $i,j,k$ :  $0.5[d(k,i) + d(k,j) - d(i,j)]$ .

- Add this minimum gain value to that calculated in Step 3.

In our example, the gain of adding Species E to the set A,C,D is 4 and PD of the set A,C,D,E is  $7 + 4 = 11$ .

*Step 5*

- Repeat Step 4 for each additional species present in the dataset.
- When no further species are recorded as present in the dataset, output results from Step 5 to file.

For our sample, the PD of the four species recorded as present is 11, or 78.6% of that possible if the full complement of five species were present.

**ABUNDANCE DATA AND CALCULATION OF  $\Delta nPD$**

Now let us consider a situation where we have relative or absolute abundance data for each of the five species potentially present at the site (Fig. 2).

This dataset can be viewed as comprising three presence/absence subtrees, illustrated in Figure 2(iii)–(v). The minimum spanning path (PD) is calculated for each of the three subtrees, using Steps 1–5 outlined earlier for presence/absence data. In this sense, presence/absence data is a special case where all species, when present, are equally abundant in the sample.

If we apply Steps 1–5 from above to each of the subtrees (Fig. 2iii–iv), we have:

*Subtree 1* (Fig. 2iii):

Minimum spanning path (= PD)

$$= d(A,C) + 0.5[d(D,A) + d(D,C) - d(A,C)] + 0.5[d(E,A) + d(E,C) - d(A,C)] = 11$$

*Subtree 2* (Fig. 2iv):

Minimum spanning path (= PD)

$$= d(A,D) + 0.5[d(E,A) + d(E,D) - d(A,D)] = 10$$

*Subtree 3* (Fig. 2v):

Minimum spanning path (= PD) =  $d(A,E) = 7$

In aggregate these three subtrees have a minimum spanning length of  $11 + 10 + 7 = 28$ .

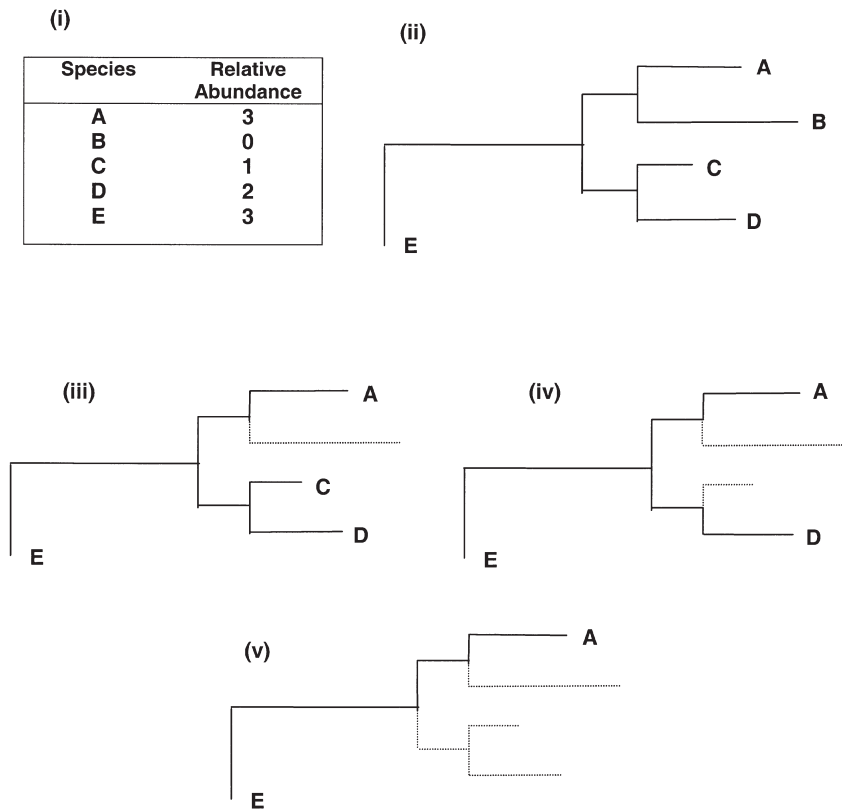
This phylogenetic diversity measure that allows utilization of abundance data, is here termed  $\Delta nPD$ . As a measure of community structure,  $\Delta nPD$  takes into account both the option values contributed by the species present and the relative abundance of each. It bridges the gap between ecological diversity measures, which emphasize species richness and abundances but are insensitive to species differences, and phylogeny-based diversity measures that emphasize evolutionary differences and species richness but are insensitive to species abundances (Ganeshaiyah *et al.*, 1997; Ganeshaiyah & Shaanker, 2000; Izsák & Papp, 2000; Warwick & Clark, 2001). The abundance-weighted measure,  $\Delta nPD$ , also provides an approximation of loss minimization (*sensu* Weitzman, 1992; Witting, McCarthy & Loeschcke, 1994; Witting, Tomiuk & Loeschcke, 2000) under the assumption that the extinction probabilities of the different species are reflected in their abundances (e.g. Gilpin & Soulé, 1986; Soulé, 1987; Boyce, 1992).

As an approach to calculation of biodiversity option value of communities,  $\Delta nPD$  is clearly sensitive to the total numbers of individuals in the sample. This is appropriate only if a standard methodology is used when sampling different communities or when sampling the same community repeatedly over time.

**ABUNDANCE DATA AND CALCULATION OF  $\epsilon nPD$**

Analogous to the important measures of compositional heterogeneity in ecological analyses (e.g. the dominance index  $N_{max}/\Sigma N$  of Berger & Parker, 1970), it may be of interest to examine the dispersion of option value contributions in the community. Such an interest may arise, for example, when land-use activities favour increased abundance in common species while distinctive, vulnerable species are driven towards local extinction. An analysis of temporal trends in the dispersion of option values is likely to be valuable in developing loss minimization strategies. A pragmatic approach to quantifying the evenness of option value contributions, here termed  $\epsilon nPD$ , is to compute the ratio of  $\Delta nPD$  for the sampled community to that expected from a null community where individuals are evenly distributed among the species. That is

$$\epsilon nPD = \Delta nPD_O / \Delta nPD_E \tag{8}$$



**Figure 2.** Trees within trees. Where abundance data are available (i), samples can be viewed as representing multiple presence/absence subtrees (iii, iv, v) of the tree that depicts phylogenetic relationships among the species (ii). The degree to which these subtrees are complete copies of the full tree reflects the relative abundance of the species. In the subtree depicted in (iii), for example, Species A, C, D and E are each represented with a relative abundance of 1, while species B is not represented due to its zero abundance. This subtree is a complete copy of the tree depicted in (ii) except that the branch to Species B is not represented. The PD scores of subtrees can be summed to estimate the PD of the community.

where  $\Delta nPD_O$  is the observed abundance-weighted PD defined above for  $n$  individuals drawn from species pool  $Q$ , and  $\Delta nPD_E$  is the expected  $\Delta nPD$  where  $n$  individuals are distributed perfectly even among all species in species pool  $Q$ . Note that  $Q$  is the total species pool from which individuals are potentially drawn when sampling, and not the pool of species represented in the samples.

An  $enPD$  approaching unity indicates all individuals contribute equally to the feature diversity and thus option values of the community. Departures from unity indicate dominance in the sampled community. An  $enPD$  approaching zero indicates a predominance of species with below average contributions to feature diversity or biodiversity option value, while an  $enPD$  exceeding unity indicates a predominance of species with above average contributions to feature diversity.

Perfect evenness in  $n$  individuals among all  $Q$  species can be shown by randomization permutations to average  $n/Q$  abundance for all species in  $Q$ . We can also show that over a large number of randomization

permutations,  $\Delta nPD_E$  for  $n$  individuals among all  $Q$  species, is given by

$$\Delta nPD_E = PD_Q(n/Q). \quad (9)$$

This is consistent with the subtree summation methodology for calculation of  $\Delta nPD$  described above, although space does not merit illustration here.

#### SELECTION OF INDICATOR SPECIES

Given that the information of interest is feature diversity or option value, it follows from eqn (7) that the species with the highest contribution to PD in the species pool  $Q$  also provides the highest information content. Loss (extinction) of that species would impose the greatest loss of features or evolutionary information, among all species in pool  $Q$ . All other things being equal, we should therefore regard the species with the highest individual contribution to feature diversity as the most preferred indicator of total feature diversity or information content of pool  $Q$ .

Intuitively, this reasoning can be extended to the multispecies situation. For any given subset of species  $S$  from the species pool  $Q$ , the indicator value is given by

$$IV_S = PD_S/PD_Q. \tag{10}$$

In selecting an indicator species set, the task is essentially that of identifying the smallest subset of species  $S$  for a given  $IV$ . That is, maximize  $IV_S$  while minimizing  $S$ .

We can evaluate the indicator value or information content of the indicator species set by plotting the cumulative information statistic,  $IV$ , for indicator species sets  $I_k, I_k + I_l, I_k + I_l + I_m \dots$  through to  $I_Q$ . Plotting the cumulative information allows us to select the appropriate indicator set. The selection of an indicator set is most robust where the cumulative information is asymptotic, such that we may select the indicator species based on some cut off near the asymptote. Where the cumulative information is linear throughout, species contribute equally and therefore an indicator subset cannot be selected.

EXPECTED LOSSES AND GAINS IN OPTION VALUE

As shown above, the  $\Delta nPD$  methodology enables detection of changes in phylogenetic diversity or option value at the community level brought about by relative changes in abundance of species. This is a retrospective analysis. However, management of biodiversity often requires prospective analyses and optimization procedures for minimization of future loss of biological diversity. Here I show that  $\Delta nPD$  provides a framework for integration of an evolutionary evaluation with an ecological multispecies risk analysis.

Following Witting *et al.* (1994, 2000), risk analysis requires estimates of the probability that species will survive, or conversely become extinct, within some defined time period. Let us consider a situation where the probabilities of survival in the different species in the face of threats associated with human activities are independent. This could be the case if the population dynamics of the different species are uncorrelated. Let  $s_{kz}$  be the expected survivorship of species  $k$  in the presence of threat  $z$ . The expected survivorship  $E(S)$  of species  $k$  in the face of multiple threats, denoted by  $z = z_1, z_2, \dots, z_n$ , can then be calculated by probability multiplication

$$E(S)_k = s_{kz_1} \cdot s_{kz_2} \dots s_{kz_n}. \tag{11}$$

These  $sz$  coefficients can themselves be estimated by the relationship between population viability and one or more parameters of the biotic and abiotic environments, although there has long been recognition of the difficulty in estimating the relative importance of

contemporaneous or sequentially acting agents of mortality in populations (e.g. Morris, 1965; Buonaccorsi & Elkinton, 1990; Elkinton *et al.*, 1992). Witting *et al.* (1994, 2000) provide equations for calculating probabilities when survivorship among species are correlated or indeed causally linked.

The potential benefit of biodiversity management is the difference with and without constraint on species survival imposed by human resource use activities. Species with low survival expectation, that is low  $E(S)$ , can reasonably be expected to offer the greatest urgency for conservation management, where the potential gains in survivorship are  $1 - E(S)$ . The species that offers the highest combination of high option value and high potential for increase in survivorship constitute the highest merit,  $m$ , for management intervention; thus

$$m_k = 1 - E(S) \cdot d(k, Q \setminus k), \tag{12}$$

where, as defined above,  $E(S)$  is the survival expectation of species  $k$  in the presence of multiple threats, and  $d(k, Q \setminus k)$  is the phylogenetic distance of species  $k$  from all other species in the set  $Q$  calculated using eqn (1) or read from a matrix of pairwise distances. Note that in the special situation where we are considering merit among all species – that is, where  $Q = T$  – the  $d(k, Q \setminus k)$  component of eqn (11) is equivalent to  $PD_{SUk}$  defined in eqn (2).

Let  $mPz$  denote the merit associated with a particular management project,  $Pz$ , which seeks to increase the survivorship probability of a species through reduction or elimination of threat  $z$  operating against that species. The merit score for project  $Pz$ , focused on species  $k$ , is given by

$$mPz = s_{kz} - s_{k0} \cdot d(k, Q \setminus k), \tag{13}$$

where  $s_{k0}$  is the survival coefficient of species  $k$  in the absence of management.

In most real-world situations, survivorship in different species is correlated. Therefore, particular projects will often have consequences for more than one species. Furthermore, the simple summation of merit scores for the different species is not appropriate because the option value of a group of species is the minimum spanning path between those species, rather than just the sum of their unique branch lengths. The  $\Delta nPD$  methodology provides a means of assessing project merit consistent with the philosophy underpinning eqn (12) and with general application across single and multiple species situations.

Let  $MPz$  denote the benefit associated with a particular management project,  $Pz$ , that modifies the survivorship probability of one or more species through reduction or elimination of threat  $z$  operating against one or more of those species. Let  $Nz$  be the benefit from a portfolio of such projects. Generally an increase in

survivorship probability is manifest in increased mean abundance. Therefore we can express benefit as

$$MP_z = \Delta nPD_{P_z} - \Delta nPD_{P_0} \quad (14)$$

and

$$N_z = \Delta nPD_{P_a} - \Delta nPD_{P_0}, \quad (15)$$

where  $P_z$  is the situation with management of threat  $z$ ,  $P_a$  is the situation under a portfolio of projects that manage multiple  $z$  threats, and  $P_0$  that without management. In calculating  $\Delta nPD$ , the expected survivorship coefficients are incorporated simply by multiplying initial abundance of each species by the proportional expected survivorship  $sz$  or  $E(S)$ .

Let  $cP_z$  be the cost of project  $P_z$ . Given a total budget of  $F$ , the simplest form of constrained expected diversity-maximizing problem might be

$$\begin{aligned} &\text{Maximize } N_z \\ &\text{Subject to } \sum cP_z = F. \end{aligned} \quad (16)$$

When the budget constraint is not being met, such that  $\sum cP_z > F$ , optimal allocation of the conservation budget proceeds by eliminating the least beneficial project, one project at a time, until the budget constraint is just met. The least desirable project, across all species and project combinations, is given by

$$\text{Minimize } \{MP_z/cP_z\}. \quad (17)$$

Under this 'greedy' algorithm, the portfolio of projects is reduced until the budget constraint is met, resulting in probability of survival of species being brought down towards zero. Where survival probability of a species is reduced to zero, as a consequence of rejecting one or more projects, then a new species set  $Q$  is defined.

Alternatively, the most cost-effective portfolio of projects may be found by maximizing complementarity of projects from the perspective for option values while minimizing costs. That is,

$$\begin{aligned} &\text{Maximize } N_z / \sum cP_z \\ &\text{Subject to } \sum cP_z = F. \end{aligned} \quad (18)$$

## APPLICATION OF PD TO CONSERVATION MANAGEMENT: AVIAN CASE STUDIES

### SYSTEMATIC FRAMEWORK

The DNA–DNA hybridization study of Sibley & Ahlquist (1990) served as the primary source of dissimilarity information for computation of PD for the entire global avian fauna or for different subsets of those species now or previously resident in the New Zealand region.

The essence of DNA–DNA hybridization is to compare the genomic similarity between any two species. Briefly, DNA is taken from one of the species to be tested, cut into lengths of about 500 base pairs, and double-strand molecules separated into two single strands. These single strands of DNA are made radioactive, and are then known as tracer DNA. They are added to a large excess of single stranded DNA from the second species, known as the driver DNA. The mixture is allowed to anneal, during which strands of tracer DNA will form double strands (or hybridize) with strands of driver DNA where their sequences are sufficiently similar. The more similar they are, the more tightly they will hybridize. The duplex formed by annealing is then subjected to gradually increasing temperatures, which progressively splits the double stranded fragments apart. This dissociation is measured as the loss of radioactivity at each step in temperature and the melting curve is a graphical representation of the increasing percentage of single-stranded tracer DNA associated with rise in temperature. The dissociation midpoint ( $T_{50H}$ ) is taken as a measure of the overall genetic divergence. The delta  $T_{50H}$  values are believed to be relative to time, with attempted calibrations suggesting  $T_{50H} 1.0 = 2.3$  Myr. While no simple relationship may exist between  $T_{50H}$  values and absolute time, owing to possible differences among lineages in rates of evolution and other factors (Sibley, Ahlquist & Monroe, 1988; Bleiweiss, Kirsch & LaPointe, 1994), Bleiweiss *et al.* (1995) concluded that rate variation does not greatly affect recovery of the phylogeny from analysis of delta  $T_{50H}$  values as estimates of relative divergence times.

The phylogenetic reconstruction made by Sibley & Ahlquist (1990) was based on manual implementation of unweighted pair-group arithmetic averages linkage (UPGMA) clustering of about 26 554 DNA hybridization experiments using 1069 species of birds, of which 310 were radio-labelled tracers. With a total of about 9700 recognized extant bird species in the world, the result is that less than 4% of the possible species pair comparisons were made. Notwithstanding this, the phylogenetic study of Sibley & Ahlquist (1990) represents the most extensive sampling, using a standardized methodology, yet produced for birds.

As acknowledged by Sibley & Ahlquist (1990), the delta  $T_{50H}$  values as estimates of relative divergence times are most robust at higher taxonomic levels, i.e. the strength of their work is in the elucidation of divergence patterns at the family level and above. Bleiweiss, Kirsch & Matheus (1994) and Bleiweiss *et al.* (1995) supported the use of the Sibley & Ahlquist phylogeny for the branching order between the major clades of birds. Hedge & Sibley (1994) found a high correlation between estimates of divergence among a selection of Ciconiiformes birds from

DNA–DNA hybridization and a 1.7-kb of aligned sequence from 12S and 16S rRNA. What is lacking in Sibley & Ahlquist's (1990) study is mainly information about divergence patterns towards the terminus of branches within clades, and in particular the placement of the species not included in their DNA hybridization experiments. In the present study, supertree methodologies (Sanderson *et al.*, 1998; Bininda-Emonds *et al.*, 1999) were used to combine other phylogenetic reconstructions with that proposed by Sibley & Ahlquist (1990), thus providing a more complete, terminal branch sampling of the World avian fauna from which to compute distances between all species pairs. Essentially, the tree proposed by Sibley & Ahlquist was used as a 'backbone' constraint tree, and matrix representation using parsimony analysis (MRP) and average consensus (AC) procedures was used here to add genera and species not included in the Sibley & Ahlquist study while enhancing resolution of relationships within families. Briefly, MRP represents the pattern of relationships within a source tree as a series of binary elements ('characters') describing each node in turn. Descendants of a node are scored as '1', all others (except taxa missing from that source tree which receive '?') as '0' (Baum, 1992; Ragan, 1992). Matrices were constructed using Excel spreadsheets. A hypothetical all-zero outgroup was added to each matrix to polarize the elements. All matrices were analysed using PAUP\* 4.0 (Swofford, 1998). The exact branch-and-bound algorithm was used for matrices with fewer than 20 taxa. For larger matrices, I used the approximate heuristic algorithm with a random addition sequence (25 repetitions), TBR branch swapping on minimal trees only (steepest descent on), collapsed zero length branches, and unlimited MAXTREES. Equally most-parsimonious solutions were summarized using strict consensus. The average consensus procedure (LaPointe & Cucumel, 1997) is an optimization-based method that returns a consensus-weighted tree (i.e. a tree with branch lengths) that is 'closest' to a set of input weighted trees. The method proceeds in three steps. First, the trees to be combined are standardized by bounding distances between 0 and 1. Second, relative distances between the average of the path-lengths matrices corresponding to the trees to be combined is computed. Third, a least-squares algorithm is applied to this average matrix to obtain a consensus solution.

In the absence of published cladograms, taxa were manually placed within the tree topology in accordance with current taxonomy summarized in Sibley & Ahlquist (1990) and Sibley & Monroe (1990). With speciose groups, the taxa were often added as unresolved polychotomies. Recognizing that different lineages may be evolving at different rates (Gillespie, 1991; Wayne, van Valkenburgh & O'Brien, 1991; Flynn, 1996) and

that rate of change may decrease with increasing divergence times (Wayne *et al.*, 1991; Gittlerman *et al.*, 1996), the concept of a local molecular clock (Bailey *et al.*, 1991) was applied. Accordingly, divergence times for the added taxa were set to values corresponding to the mean of taxa sampled within the same Order by Sibley & Ahlquist (1990).

The publications of Sibley & Monroe (1990, 1993) (including the electronic versions on the Internet; e.g. de By, 1999a) were used as the primary sources of information on species assignments to genera and higher taxonomic categories. These were supplemented by Internet databases on more recently recognized species (e.g. de By, 1999b) and recent compilations for modern avian extinctions (World Conservation Monitoring Centre, 1992; Collar *et al.*, 1994; R. Holdaway, pers. comm., 1999). The nomenclature used here largely follows that of Sibley & Ahlquist (1990) and Sibley & Monroe (1990, 1993), except that generic and species nomenclature of birds of the New Zealand region follows that Marchant & Higgins (1990, 1993), Higgins (1999), Higgins & Davies (1999), with modifications noted by Holdaway, Worthy & Tennyson (2001).

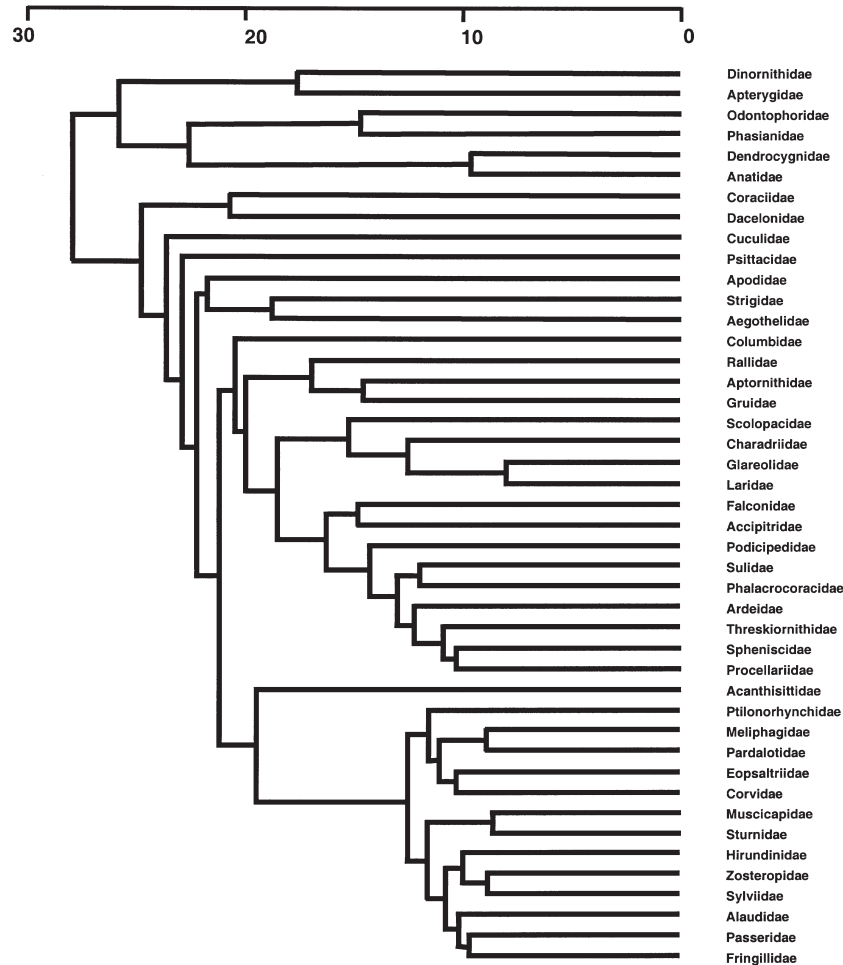
The data generated for the entire modern global avian fauna were stored as a matrix of species pairwise divergence distances, with distances equivalent to  $\Delta T_{50H}$  values  $\times 10$ . This distance matrix is available from the author. A cladogram depicting relationships among the avian families represented in New Zealand is presented in Fig. 3.

#### STATE OF THE ENVIRONMENT REPORTING

##### *Background*

The 1993 ratification of the International Convention on Biodiversity (CBD) confirmed New Zealand's ongoing commitment to the international effort to conserve global biological diversity through appropriate protection activities and sustainable use. Two recent keystone documents, *The State of New Zealand's Environment 1997* (Ministry for the Environment, 1997) and *The New Zealand Biodiversity Strategy* (Department of Conservation & Ministry for the Environment, 2000), identified decline in biological diversity as New Zealand's most pervasive environmental issue. Both documents signal a need for and a commitment to development and implementation of a core set of indicators of biodiversity.

New Zealand's national system for reporting on the State of the Environment (SOE) is being developed by the Ministry for the Environment in collaboration with other agencies. It is known as the *Environmental Performance Indicators Programme* (EPIP). Environmental performance indicators are agreed measures that help to track changes in the environ-



**Figure 3.** A cladogram illustrating phylogenetic relationships among New Zealand birds (indigenous and introduced), taken as an illustrative sample from a phylogeny constructed for the global avian fauna by supertree procedures (see text for further details).

ment and monitor success (or otherwise) of the nations environmental policies and legislation. A core set of environmental performance indicators was implemented by Ministry for the Environment in 2000, including those relating to biodiversity. Other indicators are still under development (see [www.environment.govt.nz](http://www.environment.govt.nz)).

Environmental performance indicators are being developed within the *Pressure-State-Response* model (Organisation for Economic Co-operation and Development, 1993). Indicators of the *state of biodiversity* generally focus on changes in species richness at the national level, which reflect extinctions or re-introductions. Species richness as an indicator of state of biodiversity fails to recognize that all species are not equal in their contribution to global biological diversity and option values. Indicators of *pressure on biodiversity* tend to focus on gross changes in the extent and quality of habitat, but frequently fail to inform

about pressures acting differentially on species that vary in contribution to global biological diversity and option values. In the first avian case study, I demonstrate the utility of PD in monitoring and reporting on changes in biodiversity option value that reflects changes in the composition of the biota. Furthermore, I show that  $\Delta nPD$  provides a framework for weighting measures of habitat extent to better reflect the pressures on option values.

#### Method

Species richness and PD were used as measures of marginal contributions to avian diversity at various spatial scales. First, contributions of the faunas of the entire New Zealand archipelago (Kermadec Islands through to Campbell Island, inclusive of waters of the continental shelf) and the Waikato region (a local government region within the North Island) to global avian diversity were calculated. Next, contributions of

species in different residency categories (vagrants, migrants, nonendemic natives, endemics, introduced) were calculated for the New Zealand and Waikato faunas. Marginal contribution was defined as the loss of species richness or PD that would occur if the fauna in question were to become extinct. Data on the global avian fauna was derived from the compilations employed in the reconstruction of avian phylogeny, described above, with separate species checklists for c. 2000 BP and current (AD 2000). Species presence in the New Zealand archipelago and the Waikato region for these two points in time were derived from a variety of literature sources (e.g. Bull, Gaze & Robertson, 1985; Marchant & Higgins, 1990, 1993; Turbott, 1990; Heather & Robertson, 1996; Harvey, 1999; Higgins & Davies, 1999; Higgins, 1999; Holdaway *et al.*, 2001) and personal communication with ornithologists and palaeontologists (see Acknowledgements). In the case of the New Zealand and Waikato faunas, 2000 BP equates to the period prior to human occupation. Species richness was simply the tally of the species present, while PD was calculated from species presence data using eqn (1).

Changes in habitat availability were estimated as indicators of pressures on avian biodiversity in the Waikato region brought about by human modification of the indigenous vegetation in the landscape. For each bird species in the Waikato fauna the following estimates were made: (i) extent of habitat in the Waikato prior to human intervention (c. 2000 BP); (ii) extent of habitat available in the contemporary Waikato landscape; and (iii) extent of available habitat in the contemporary Waikato actually occupied. The spatial extent of suitable habitat was then used as a surrogate of the relative abundance of birds within the Waikato region in the calculation of  $\Delta$ PD, thus proving a means of weighting habitat availability based on the differential option value of the species.

The extent of habitat of various types in the Waikato region prior to human settlement was estimated in a three-stage process using ArcView geographical information systems software. First, areas within the region differing in environmental character – environmental domains – were identified. Briefly, the region was depicted as pixels of 200-m resolution in a digital elevation model (DEM), environmental characteristics were determined for each pixel from a range of data sources, and pixels then clustered into 40 groups (domains) on the basis of environmental similarity using the Gower metric (Sneath & Sokal, 1973) of environmental distance. The environmental data comprised seven climate variables and five landform variables. (The reader is referred to Leathwick, Overton & McLeod (2002) for more detail on environmental domains classifications for New Zealand.)

Secondly, the indigenous vegetation cover was estimated. Forest composition in each environmental domain was reconstructed from spatial prediction of canopy tree abundance onto the 200-m DEM using Generalized Additive Models of species–environment relationships developed by Leathwick, Whitehead & McLeod (1996) and Leathwick (1998a,b, 2002). For non-forest systems, reconstructions were based on knowledge of current relationships between climate, landform, and broad successional patterns. The extent of larger wetlands was reconstructed largely from peat deposits as mapped on 1:250 000 scale geological maps (Kear, 1960; Schofield, 1967). These reconstructions were validated by reference to published forest (e.g. Nicholls, 1970, 1971, 1974, 1976, 1979; Clarkson & Clarkson, 1993), non-forest (Atkinson, 1981; Leathwick, 1990a,b) and lake-margin (Champion, Winton & de Lange, 1993) maps. Thirdly, the types of habitat utilized by each bird species were determined from published ecological and palaeoecological information and translated to presence/absence data for each environmental domain. From simple summation of the areas of the domains presumed occupied, an estimate was derived for extent of habitat of each species at 2000 BP.

The contemporary extent of indigenous habitat was calculated for each species (including that applicable to extinct species should they have persisted to the present) from data on portion of domains presumed occupied at 2000 BP that remain under indigenous vegetation. The data describing current land cover were derived from *New Zealand Land Resource Inventory* (Newsome, 1992) and *Landcover Database* (Terralink New Zealand, 1996). Where part or whole of a domain had been converted to systems dominated by exotic vegetation (e.g. plantation *Pinus* forests, pastoral grasslands, urban areas), assessment was made on suitability for occupancy and habitat extent accordingly calculated from data on the proportion of the domain in that particular land cover. The extent to which habitat available in the contemporary landscape is actually occupied by species at the present time was estimated from an updated digital form (Harvey, 1999) of *The Atlas of Bird Distribution in New Zealand* (Bull *et al.*, 1985) overlaid on the environmental domains depiction of the Waikato region.

In compiling the faunal lists, species that visit New Zealand as vagrants or migrants were treated as part of the New Zealand indigenous fauna. Species known as vagrants or migrants in historical times were assumed to have visited the New Zealand region in a similar fashion prior to human occupation. This stance is taken because the New Zealand region may constitute part of the species' range that is important to continuance of the species and/or the visiting species may potentially have a significant impact on the func-

tioning of the New Zealand ecosystems. The inclusion of these species in the New Zealand list clearly increases the PD scores for the New Zealand region, but does not increase the regions' contribution to global PD because the species in question are not dependent on New Zealand as habitat.

#### Results and discussion

Table 1 provides data on the contribution of species in different residency categories to species richness and PD for the entire New Zealand archipelago and for the Waikato region, both at 2000 BP (prehuman settlement) and at the present. From the 2000 BP baseline, species richness in the New Zealand avian fauna has declined. A substantial level of extinction in endemic species has been offset only partially by natural establishment and deliberate introduction of species from other faunal regions. The phylogenetic diversity of the New Zealand fauna has increased slightly from the 2000 BP baseline, mainly as a consequence of the marginal contribution of the introduced species. From an indigenous biodiversity perspective, the major concern is the loss of phylogenetic diversity as a consequence of extinction in the endemic component of the fauna. Considerable option value has been lost from the endemic fauna.

The Waikato region has witnessed an increase in

both species richness and phylogenetic diversity during the period from 2000 BP to the present. This has been largely the result of introduction of species from other faunal regions, and has occurred in despite of decline in the native fauna. The Waikato did not have an endemic fauna.

These types of analyses may provide the basis for monitoring and reporting changes in the status of the New Zealand avian fauna. In addition to tracking changes relative to baselines, it may be appropriate to monitor changes relative to that occurring globally. One approach is to report marginal contributions to the World fauna in both species richness and phylogenetic diversity. Such an analysis is presented in Table 2. As a result of human activities over the past two millennia, the World avian fauna has declined by 184 species, or 1.88%. This equates to 1.49% loss in phylogenetic diversity (also see von Euler, 2001). Over the same time period, the marginal contribution of the New Zealand fauna has declined by 41.8% in terms of species richness, and by 44.0% in terms of phylogenetic diversity. The rate of loss in biodiversity option value in New Zealand therefore greatly exceeds the global average. From a pragmatic perspective, reporting at the national level will almost invariably require collation and summation of regional data. The Waikato data are included in this analysis (Tables 1

**Table 1.** Species richness and phylogenetic diversity of the entire New Zealand avian fauna, and that of the Waikato Region, with level of contribution from species in different status categories

	Species richness		Phylogenetic diversity	
	2000 BP	Current	2000 BP	Current
New Zealand avian fauna:	313	308	8034	8194
Marginal contributions <sup>a</sup> : Vagrant species	71	70	1592	1546
Migrant native species	29	31	414	439
Non-endemic native species	78	91	1320	1508
Endemic species	135	78	3160	1593
Introduced species	–	39	–	1348
Waikato Region avian fauna:	234	246	6838	7256
Marginal contributions <sup>1</sup> : Vagrant species	105	104	2030	2006
Migrant native species	23	25	350	364
Non-endemic native species	106	83	3130	1986
Endemic species	0	0	0	0
Introduced species	–	34	–	1256

<sup>a</sup>Marginal contribution calculated as the loss in species richness and phylogenetic diversity (tree branch length) when species in particular category are deleted from tree for the fauna as a whole.

**Table 2.** Species richness and phylogenetic diversity of the World Recent and extant avian faunae, with level of contribution from the entire New Zealand fauna and that from the Waikato region

	Species richness	Phylogenetic diversity
World Recent avian fauna:	9813	532440
Marginal contribution from New Zealand <sup>a</sup>	134 (1.36%)	2340 (0.44%)
Marginal contribution from Waikato <sup>a</sup>	0	0
World extant avian fauna:	9629	524490
Marginal contribution from New Zealand <sup>a</sup>	78 (0.81%)	1310 (0.25%)
Marginal contribution from Waikato <sup>a</sup>	0	0

<sup>a</sup>Marginal contribution calculated as the loss in species richness and phylogenetic diversity (tree branch length) when New Zealand or Waikato regionally endemic faunas were deleted from that of the world fauna.

**Table 3.** Estimates of extent of ecosystem types (ha × 100) available to the avian fauna of the Waikato region, New Zealand, as habitat in 2000 BP and currently

	2000 BP	Current
Marine nearshore shelf	22930	22930
Marine shore	118	100
Estuaries	250	190
Coastal dunes	59	2
Freshwater wetlands	1100	296
Freshwater open water bodies	800	942
Indigenous coastal forest	5862	1989
Indigenous lowland forest	12248	1957
Indigenous lowland secondary scrubland	110	929
Indigenous montane forests	3689	1422
Indigenous montane grasslands and scrublands	407	85
Exotic grasslands and scrublands	0	13622
Exotic plantation forestry	0	2888
Urban	0	203
Total	24525	24525

and 2) to illustrate how regional patterns can differ from that at the national level and thus provide insights into trends at a scale more appropriate for biodiversity management.

The other aspect of SOE reporting is that of monitoring environmental pressures on biodiversity. We can assume that prior to human intervention in New Zealand ecosystems, individual bird species were broadly in equilibrium with the extent of available habitat and natural population regulatory factors such as food quality and predation. We can estimate the probable extent of favourable habitat prior to human settlement and we can assume that, in the ecological time frame of this particular analysis, species had zero

probability of extinction. Table 3 presents an analysis of changes over the past two millennia in the spatial extent of the major categories of ecosystems in the Waikato, indicative of pressures on the avian fauna associated with habitat loss. Significant losses in extent have occurred in all major indigenous ecosystems (i.e. coastal dunes, freshwater wetlands, forest, and montane grasslands/scrublands). These losses reflect land use for agriculture, plantation forestry and urban settlement, and include a substantive area that has reverted to secondary scrubland.

The consequences of these habitat losses and conversions for the Waikato avian fauna as a whole and for a selected subset of species is summarized in

**Table 4.** Estimates of habitat extent and occupancy for selected species and averaged across all species in the avian fauna of the Waikato region, New Zealand<sup>a</sup>

	Habitat extent (ha × 1000)			Proportion of 2000 BP habitat	
	Available 2000 BP	Currently available	Currently occupied	Currently available	Currently occupied
<i>Malacorhynchus scarletti</i> Olson (Anatidae)	66	4	0	0.06	0.00
<i>Cnemiornis gracilis</i> Forbes (Dendrocygnidae)	160	79	0	0.49	0.00
<i>Coturnix novaezealandiae</i> Quoy & Gaimard (Phasianidae)	623	372	0	0.60	0.00
<i>Aptornis otidiformis</i> (Owen) (Aptornithidae)	1750	876	0	0.50	0.00
<i>Coenocorypha barrierensis</i> Oliver (Scolopacidae)	1818	879	0	0.48	0.00
<i>Dinornis novaezealandiae</i> Owen (Dinornithidae)	2012	739	0	0.37	0.00
<i>Strigops habroptilus</i> Gray (Psittacidae)	2020	739	0	0.36	0.00
<i>Traversia lyalli</i> Rothschild (Acanthisittidae)	2081	1030	0	0.49	0.00
<i>Turnagra tanagra</i> (Schlegel) (Turnagridae)	2081	1029	0	0.49	0.00
<i>Sceloglaux albifacies</i> (Gray) (Strigidae)	2086	1032	0	0.49	0.00
<i>Porphyrio mantelli</i> (Owen) (Rallidae)	2086	741	0	0.36	0.00
<i>Anas chlorotis</i> Gray (Anatidae)	2143	715	0	0.33	0.00
<i>Gallirallus australis</i> (Sparrman) (Rallidae)	1824	319	1	0.17	<0.01
<i>Notiomystis cincta</i> (Du Bus) (Meliphagidae)	2081	741	2	0.35	<0.01
<i>Porzana tabuensis</i> (Gmelin) (Rallidae)	60	2	2	0.03	0.03
<i>Hymenolaimus malacorhynchos</i> (Gmelin) (Anatidae)	2107	814	89	0.39	0.04
<i>Callaeas wilsoni</i> (Bonaparte) (Callaeidae)	2020	739	218	0.36	0.11
<i>Petroica australis</i> (Sparrman) (Eopsaltriidae)	2020	1028	221	0.51	0.11
<i>Apteryx australis</i> Shaw & Nodder (Apterygidae)	2020	1028	227	0.51	0.11
<i>Gallirallus philippines</i> (Linnaeus) (Rallidae)	160	79	18	0.49	0.11
<i>Acanthisitta chloris</i> (Sparrman) (Acanthisittidae)	2081	1028	275	0.49	0.13
<i>Nestor meridionalis</i> (Gmelin) (Psittacidae)	1963	631	372	0.32	0.19
<i>Anthornis melanura</i> (Sparrman) (Meliphagidae)	2081	1050	462	0.50	0.22
<i>Falco novaeseelandiae</i> Gmelin (Falconidae)	2012	738	460	0.37	0.23
<i>Hemiphaga novaeslandiae</i> (Gmelin) (Columbidae)	1750	608	608	0.35	0.35
<i>Aythya novaeseelandiae</i> (Gmelin) (Anatidae)	100	78	37	0.78	0.37
<i>Rhipidura fuliginosa</i> (Sparrman) (Monarchidae)	2086	1052	1052	0.50	0.50
<i>Chrysococcyx lucidus</i> (Gmelin) (Cuculidae)	2012	2410	1027	1.20	0.51
<i>Halcyon sancta</i> Vigors & Horsfield (Alcedinidae)	2294	2569	2569	1.12	1.12
<i>Tadorna variegata</i> (Gmelin) (Anatidae)	2173	2469	2469	1.14	1.14
<i>Gerygone igata</i> (Quoy & Gaimard) (Acanthizidae)	2081	2412	2412	1.16	1.16
<i>Anthus novaeseelandiae</i> (Gmelin) (Motacillidae)	237	1553	740	6.55	3.12
Mean for all species	936	590	374	0.63	0.40
Mean for species resident at 2000 BP and extant today	761	602	310	0.79	0.41

<sup>a</sup>Only those species resident in the Waikato fauna at 2000 BP (i.e. excludes vagrants) and utilizing terrestrial habitat (i.e. excludes pelagic species nesting outside New Zealand region) were included in the analysis

Table 4. Averaged across all species, of the 936 000 ha habitat estimated to be available in 2000 BP, only 63% or 590 000 ha is presently available in the contemporary Waikato landscape, and only 40% or 374 000 ha is presently occupied. As illustrated in Table 4, the indicated pressures on individual bird species varies greatly. When these estimates of habitat extent are used as surrogates of abundance in the calculation of  $\Delta$ nPD, a 45% reduction in biodiversity option value is

indicated for the Waikato avian fauna as a consequence of habitat loss alone (Table 5).

This reduction in option value increases to 69% when habitat actually occupied in contemporary Waikato is used as the surrogate for abundance (Table 5), indicating substantive effects beyond that of changes in habitat extent. With habitat alteration there is both a direct and an indirect extinction effect. The direct effect is the immediate decline in species

**Table 5.** Changes in  $\Delta$ NPd of the avian fauna of Waikato region, New Zealand associated with loss of terrestrial habitat. In calculating  $\Delta$ NPd the extent of available and occupied habitat were used as surrogates for abundance in each species

Surrogate of abundance	$\Delta$ NPd (x 10 <sup>6</sup> ) <sup>a</sup>
Habitat available at 2000 BP	6563
Habitat currently available	3624 <sup>b</sup>
Habitat currently occupied	2050 <sup>c</sup>

<sup>a</sup>Only those species resident in the Waikato fauna at 2000 year BP (i.e. excludes vagrants) and utilizing terrestrial habitat (i.e. excludes pelagic species nesting outside New Zealand region) were included in the analysis. <sup>b</sup>Assumes no extinctions and therefore estimates  $\Delta$ PD decline from 2000 BP owing to changes in habitat extent. <sup>c</sup>Includes effect of species extinctions owing to habitat loss and modification.

caused by alteration of the extent of habitat required by the different species, while the indirect effect is the background extinctions occurring among the remaining species owing to changes in habitat quality (Witting *et al.*, 1994). Habitat fragmentation is a frequent associate to reduction in habitat extent, and has important consequences on population and species viability. Furthermore, both predatory and browsing mammals have reduced the quality of most terrestrial habitat for indigenous birds in New Zealand (e.g. Holdaway, 1990, 2000; Atkinson & Cameron, 1981) and may have allowed the ingress of exotic species (Diamond & Veitch, 1981). Consequent reductions in the population densities of indigenous birds may result in larger area requirements for self-sustaining populations than may be implied simply by measurement of extent of available habitat.

Extensive seabird breeding colonies occurred on both the New Zealand mainland and adjacent islands from the Pleistocene (Worthy & Holdaway, 1993, 1995, 1996; Holdaway & Worthy, 1994; Holdaway, 2000; Holdaway *et al.*, 2001). However, breeding colonies of seabirds became increasingly restricted after human contact, following a pattern common throughout the Pacific (Steadman, 1995). The likely cause of the elimination of the smaller burrow-nesting seabirds was predation by the Pacific rat (*Rattus exulans*) introduced about 2000 BP (Holdaway, 1996; Worthy, 1997). Populations of the remaining larger seabirds became increasingly restricted following the introduction of further *Rattus* species, pigs, mustelids and cats, and deforestation by European visitors and colonists over the past 230 years (Holdaway, 2000). Population

extinctions from mainland New Zealand and its inshore islands clearly impact on the PD and  $\Delta$ NPd scores for regions such as the Waikato. Because most of these seabirds are not endemic to the New Zealand region, population losses from New Zealand populations do not diminish the contribution of the New Zealand region to global avian diversity.

Many New Zealand bird species suffered from the direct effects of predation by humans, the most publicized being that of the moas (Emeidae, Dinornithidae) (Scarlett, 1979; Cassels, 1984; Anderson, 1989; Atkinson & Millener, 1991; Holdaway & Jacomb, 2000). However, the substantial discrepancy between habitat availability in 2000BP and the present indicates that many of these species would have been under substantial pressure from loss of habitat in the absence of this human predation.

#### SETTING PRIORITIES FOR THREATENED SPECIES MANAGEMENT

##### *Background*

Many New Zealand indigenous species have proved to be highly vulnerable to the novel disturbances associated with human settlement of the region. Many species have become extinct. Many others are in decline and considerable effort is directed to species protection. Given limited resources, New Zealand conservation agencies must prioritize among threatened species for conservation management activities. New Zealand has an established set of criteria for identification of threatened species and assigning them to categories of priority for conservation investment (Molloy & Davis, 1992; Molloy, Davis & Tisdall, 1994). Categorical assessments of taxonomic distinctiveness and viability are included in the criteria. In the present case study a subset of threatened New Zealand forest birds (Molloy *et al.*, 1994) are used to illustrate how PD provides a quantitative framework for prioritization among species.

##### *Methods*

A prioritization ranking among ten threatened New Zealand forest birds (Category B; Molloy *et al.* 1994) was made by applying eqn (13) to information on species' marginal contribution of option values and expected gains in survivorship from management. Marginal contribution was defined as the loss of PD that would occur if the species in question were to become extinct and thus lost from the New Zealand forest bird fauna. PD was calculated using eqn (1). Species survivorship expectations under current management regimes, and if that management was terminated, were estimated by consultation with several scientists with extensive experience with New Zealand forest bird conservation. Survivorship expect-

tations were projected for the 20-year period from 2000. The ten species were ranked in descending order of priority based on the product of marginal contribution of option values and expected gains in survival expectation.

#### Results and discussion

Among the ten threatened species evaluated (Table 6), *Mohoua ochrocephala* (Gmelin) (Pachycephalidae) and *Callaeas wilsoni* (Bonaparte) (Callaeatidae) were identified as highest priority. The analyses with respect to these two species highlight the interaction between marginal contributions of option value and expected survivorship gains. *Mohoua ochrocephala* offers relatively low marginal contribution, because passerine species are well represented in the New Zealand forest bird fauna, yet the continuance of current management provides for substantial gains in survivorship expectation. In the case of *Callaeas wilsoni*, marginal contribution is higher because of the high relative distinctiveness of the species, yet current management offers modest increases in the species' survival expectation.

This case study illustrates the principal of integration of an evolutionary evaluation with an ecological risk analysis. The robustness could be improved by a more quantitative species viability analysis for esti-

mation of the survival expectations. A further sophistication would be the evaluation of different management regimes, and the selection of the optimal set of management projects, through complementarity, that maximize gains in biodiversity option values for a given level of investment and project feasibility (e.g. Stephens, 1999). The key point is that PD provides a quantitative values framework for prioritization of actions.

#### MONITORING COMMUNITY RESPONSE TO MANAGEMENT

##### Background

Three case studies are used here to illustrate the application of PD to monitoring community compositional changes under three different land management regimes that are highly relevant to conservation of forest birds in New Zealand. While logging of indigenous forest has declined substantially in New Zealand over the past 30 years, there remains much concern about further loss in habitat resulting from clear felling on private land and degradation of habitat through selective logging on state-owned land. Since c. 1930 there has been extensive planting of exotic conifers, principally that of *Pinus radiata*. Conifer plantations now cover about 1.5 million ha, mostly on

**Table 6.** Priority ranking among threatened New Zealand forest bird species for conservation management, based on gains in biodiversity option value calculated as the product of marginal contributions to phylogenetic diversity and expected gains in survivorship probability from management

	Marginal contribution to phylogenetic diversity	Expected survival with current management	Expected survival with no management	Survival expectation won by current management	Biodiversity option value won by current management
<i>Mohoua ochrocephala</i> (Gmelin) (Pachycephalidae)	9	0.9	0.0	0.9	8.1
<i>Callaeas wilsoni</i> (Bonaparte) (Callaeatidae)	25	1.0	0.8	0.2	5.0
<i>Cyanoramphus forbesi</i> Rothschild (Psittacidae)	20	1.0	0.8	0.2	4.0
<i>Philesturnus carunculatus</i> (Gmelin) (Callaeatidae)	25	1.0	0.9	0.1	2.5
<i>Notiomystis cincta</i> (Du Bus) (Meliphagidae)	19	1.0	0.9	0.1	1.9
<i>Coenocorypha huegeli</i> (Tristram) (Scolopacidae)	15	0.9	0.8	0.1	1.5
<i>Apteryx haastii</i> Potts (Apterygidae)	7	1.0	0.8	0.2	1.4
<i>Falco novaeseelandiae</i> (Gmelin) (Falconidae)	76	1.0	1.0	0.0	0.0
<i>Hemiphaga novaeseelandiae</i> (Gmelin) (Columbidae)	17	1.0	1.0	0.0	0.0
<i>Nestor notabilis</i> Gould (Psittacidae)	20	1.0	1.0	0.0	0.0

land formerly in indigenous forest. There is considerable debate on the contribution of these plantations to conservation of the indigenous biota.

Invasive, alien species are now recognized as a major threat to the indigenous biota. A range of mammalian and invertebrate predators, and weeds, are managed on conservation land in an attempt to prevent further loss of indigenous biodiversity. While large areas of the conservation estate are subject to low-intensity management of alien species, there is increasing focus on highly intensive management for a range of pests at a few sites. A large portion of public expenditure on conservation in New Zealand is presently devoted to management of alien pest species. Contingent with this expenditure is the demand for demonstration of positive outcomes for biodiversity and thus there is increasing emphasis on monitoring responses to management in indigenous communities.

#### Method

The first case study draws on data from Onley (1983) on comparison of bird communities in intact and logged *Dacrydium cupressinum*/*Nothofagus truncata* indigenous forest in the vicinity of Karamea, in the South Island. The second draws on data from Clout & Gaze (1984) on comparison of bird communities in indigenous *Nothofagus* forests and exotic *Pinus radiata* forests in the vicinity of Nelson, South Island. The third case study utilizes bird community data from two indigenous broadleaf-podocarp forests in the vicinity of Te Kuiti, North Island (P. Bradfield, pers.

comm., 1999). The forest at Mapara was subject to intensive management of the introduced marsupial pest, *Trichosurus vulpecula* Kerr, using aerial (1990, 1991, 1992) and bait station (1993/94, 1996/97) application of baits containing sodium monofluoroacetate (1080). The forest at Opokonui, which received an aerial application of 1080 only in 1995, served as a low-intensity management reference site.

In all three studies, estimates of relative abundance in bird species were made using 5-minute bird counts (Dawson & Bull, 1975) at various stations within each forest. Onley (1983) made 44 5-min counts in unlogged and 37 5-min counts in logged indigenous forest during the period 6–8 June 1982. Clout & Gaze (1984) made a total of 24 5-min counts, over a 24-month period from November 1977, for 20 stations in each of six *Pinus radiata* forests and five indigenous *Nothofagus* forests. Staff from the Department of Conservation (P. Bradfield, pers. comm., 1999) made 100 5-min bird counts at both Mapara and Opokonui in June 1997. For the analyses of abundance,  $\Delta$ nPD and  $\epsilon$ nPD presented here, these 5-min bird count data were standardized to numbers per 100 min of observation. Estimates of species richness were taken directly from the numbers of bird species recorded during the 5-min counts.

#### Results and discussion

The re-analyses of the data on species richness and abundance from Karamea and Nelson (Table 7) are consistent with the conclusions of Onley (1983) and Clout & Gaze (1984) that logging and conversion to

**Table 7.** Changes in compositional structure of avian communities under different management regimes at three locations in New Zealand as indicated by 5-minute bird counts. Data standardized to means per 100 5-minute counts. See text for more detail on the management regimes

	Karamea <sup>a</sup> <i>Dacrydium</i> / <i>Nothofagus</i> forest management		Nelson <sup>b</sup> forest type		Te Kuiti <sup>c</sup> predator management	
	Unlogged	Logged	<i>Nothofagus</i>	<i>Pinus</i> plantation	Low intensity	High intensity
All species richness	18	18	20	20	17	21
Indigenous species richness	12	11	13	12	8	11
All species abundance	1686	1173	929	702	161	287
Abundance of indigenous species	1493	789	756	399	143	259
All species PD	1020	1173	1299	1313	988	1160
Indigenous PD	848	814	1048	918	565	743
All species $\Delta$ nPD	91700	58400	48700	32900	9300	15000
Indigenous $\Delta$ nPD	84000	42300	40800	18800	8500	13900
All species $\epsilon$ nPD	1.00	0.91	0.80	0.72	0.98	0.89
Indigenous $\epsilon$ nPD	0.84	0.80	0.67	0.61	0.88	0.79

<sup>a</sup> From Onley (1983). <sup>b</sup> From Clout & Gaze (1984). <sup>c</sup> From P. Bradfield (pers. comm., 1999).

*Pinus* plantations, respectively, result in substantial changes in the compositional structure of the forest bird communities. A very marked decline in abundance of indigenous species is indicated, and is only partially offset by the increase in the higher representation of introduced species. The evident decline in  $\Delta$ nPD with logging of the forests, or planting to *Pinus*, parallels that in abundance, with the potential complementarity offered by the introduced species being unable to compensate for the loss of option value occurring in the indigenous component of the communities.

At Te Kuiti, higher species richness and abundance in both total and indigenous birds were detected in the high-intensity predator management forest than in the low-intensity management forest (Table 7). Substantive increases in PD and  $\Delta$ nPD are indicated for the high-intensity management regime.

In all three studies,  $\epsilon$ nPD for the indigenous component of the avian faunas tended to be lower than for the faunas as a whole (Table 7). While the 5-minute count methodology applied to New Zealand forest systems generally yields abundance data dominated by passerine species, the introduced passerine species tends to promote evenness by contributing option values not present in the indigenous fauna.

These three case studies also serve to highlight the need for proper design in monitoring systems if robust interpretations are to be made. Of the three studies considered here, only that of Clout & Gaze (1984) had replication of the management units of interest (indigenous forests; *Pinus* forests) and thus generated data in a form amenable to statistical analysis. Indeed, statistical analyses indicate that the only differences between the indigenous forests and *Pinus* forests relate to the indigenous component of the bird communities (Abundance of indigenous species,  $P = 0.040$ ; Indigenous  $\Delta$ nPD,  $P = 0.027$ ). A number of authors have applied statistical analyses to 5-minute bird counts, using data from different stations within a single treatment block as replicates. However, this is pseudo-replication and does not provide for robust testing of treatment effects, unless repeated counts are made from the same set of stations in each system before and after treatment (Green, 1979, 1993; Stewart-Oaten, Murdoch & Parker, 1986).

#### SELECTION OF INDICATOR SPECIES

##### *Background*

An alternative strategy to documenting change in biodiversity as a whole may rely on monitoring of a subset of species. Such reliance on indicator species may be necessary when funds do not allow for sampling of the intensity required to document changes in occurrence or abundance of all species. The issue is then, how are

indicator species best selected from the pool of species known to be present? An objective approach is to select a subset of species, of specified size, that conveys the most information about the full set of species.

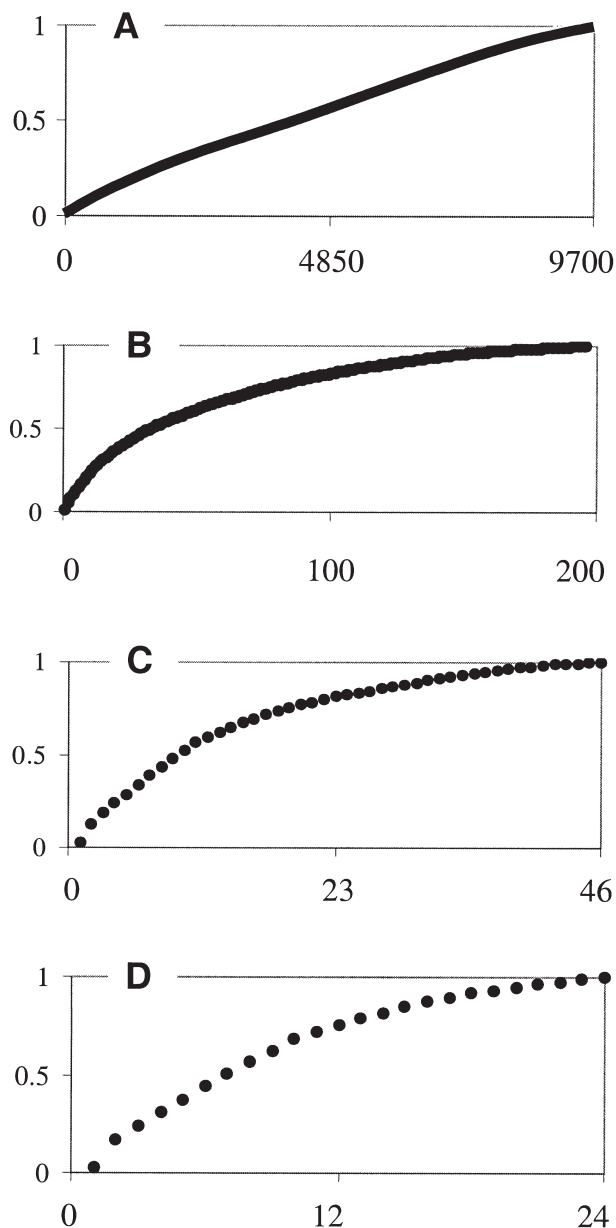
##### *Method*

Using eqn (10), indicator species sets were selected for the avian faunas at four spatial scales, namely (i) entire global fauna, (ii) entire New Zealand fauna, (iii) New Zealand forest bird fauna, and (iv) Waikato forest bird fauna. The species pool from which the indicator set was to be selected was refined for each spatial scale. An indicator species set was defined, arbitrarily, as that minimal subset that provided 50% of the cumulative information content.

The predictive power of indicator subsets selected on PD criteria were then examined by retrospective analyses of changes in the New Zealand and Waikato regional forest avian faunas over the past two millennia. This analysis assumes that indicator subsets had been selected at 2000 BP and used to monitor faunal changes over the subsequent 2000 years. Using eqn (10), subsets of 20 and 15 species were selected from the New Zealand and Waikato faunas, respectively, on the basis of contribution to total PD. Additional indicator subsets, of the same size in terms of species number, were also selected from a single random draw and from the mean of 5000 random draws. Proportional losses in species richness and PD in these indicator subsets, observed over the last two millennia, were compared with losses in the fauna as a whole. The utility of the indicator subset was determined by how closely the ratio *Observed changes in indicator set: Observed changes in entire fauna* approximated VI, the information value of the indicator. That is, if the indicator subset has a PD value 0.60 that of the entire fauna ( $VI = 0.60$ ), we would expect subsequent changes in PD of the indicator subset to be about 0.60 of the changes occurring in the fauna as a whole.

##### *Results and discussion*

Applied to the entire global avian fauna, cumulative information was linear rather than asymptotic (Fig. 4a) and therefore an informative indicator subset could not be selected. The amount of information or indicator value for a small, PD-maximizing subset depends on the kind of diversification processes that gave rise to the group under consideration. In particular, the indicator value of the PD-maximizing subset is strongly dependent on the topology of the phylogenetic tree, which, in turn, reflects the underlying variation in diversification rates across lineages within the group. Recent work has suggested that phylogenetic trees taken from the literature are often more unbalanced than those produced by equal-rate Markov and equilibrium models (reviewed by Purvis, 1996; Mooers



**Figure 4.** Curves illustrating cumulative phylogenetic diversity for PD-maximizing subsets plotted against species in rank order of inclusion in the subsets: (a) Global avian fauna; (b) Entire New Zealand avian fauna; (c) New Zealand forest bird fauna; (d) Waikato forest bird fauna. Note that in B–D 50% cumulative information is attained with substantially less than 50% of the species drawn from the respective species pools.

& Heard, 1997) and that this is most likely the result of differences in speciation rate (or past extinction rates) among extant lineages within a clade. In the case of the global avian fauna, a substantial proportion of the total information is contained in a small

number of very speciose, recently radiated clades, namely Psittacidae, Apodidae, Trochilidae, Furnariidae, Thamnophilidae, Tyrannidae, Muscicapidae, Sturnidae, Pyconotidae, Zosteropidae, Sylviidae, Passeridae, Nectarinidae and Fringillidae. That is, the phylogeny is strongly dominated numerically by species with trivial marginal contributions in option value (von Euler, 2001).

Given this highly unbalanced phylogeny, a more pragmatic approach at the global level is to constrain the pool from which indicators are selected to comprise only one species from each of the major avian clades.

The IV cumulation curves for the entire New Zealand avian fauna (Fig. 4b), the New Zealand forest bird fauna (Fig. 4c) and the Waikato forest bird fauna (Fig. 4d) are strongly asymptotic, and each provides the basis for the selection of a small subset that contributes a high proportion of the total PD. In the case of the entire New Zealand avian fauna 33 species (17%), from a total fauna of 198 species, contributed in excess of 50% of the PD. This level of indicator value is achieved with 10 (22%) and 7 (29%) for the New Zealand forest bird Waikato forest bird faunas, respectively. These indicator sets, with the cumulative IV statistics, are given in Table 8.

These case studies illustrate the application of PD as an objective, quantitative approach to selection of indicator species, where the resource of interest is biodiversity option value. Such objectivity is generally lacking in the selection of indicator species in present biodiversity management. In practice, some *a posteriori* adjustments to the selected set of indicator species may be required because cost or other factors constrain ability to monitor populations of particular species. Optimization algorithms could readily be developed to combine the PD framework with sampling considerations.

In the retrospective analysis of the changes in the New Zealand (Table 9) and Waikato (Table 10) forest avian faunas, the indicator subsets selected on the basis of PD contribution provided slight over-prediction of the losses in PD observed to have occurred over the past two millennia. By contrast, the indicator subsets selected from random draws of species grossly under predicted the amount of loss observed in PD.

## GENERAL DISCUSSION AND CONCLUSIONS

There is a rapidly growing understanding of the linkage between human development and the environment, with the associated development of a nature conservation ethic and science (The World Bank, 1997). As expressed by Bibby (1999), this offers an opportunity to bring biodiversity conservation into the mainstream of economic and land-use planning.

**Table 8.** Indicator species sets selected on the basis of cumulative proportional contribution to PD

<b>Entire New Zealand bird fauna (species pool = 198)</b>			
<i>Elsemyornis melanops</i> (Vieillot) (Charadriidae)	0.013	<i>Chrysococcyx lucidus</i> (Gmelin) (Cuculidae)	0.461
<i>Apteryx australis</i> Shaw & Nodder (Apterygidae)	0.054	<i>Prosthemadera novaeseelandiae</i> (Gmelin) (Meliphagidae)	0.469
<i>Anas aucklandica</i> (Gray) (Anatidae)	0.079	<i>Zosterops lateralis</i> (Latham) (Zosteropidae)	0.478
<i>Halcyon sancta</i> Vigors & Horsfield (Alcedinidae)	0.103	<i>Gallirallus philippines</i> (Linnaeus) (Rallidae)	0.486
<i>Eudynamis taitensis</i> (Sparrman) (Cuculidae)	0.125	<i>Cygnus atratus</i> (Latham) (Anseridae)	0.494
<i>Nestor meridionalis</i> (Gmelin) (Psittacidae)	0.148	<i>Oceanites nereis</i> (Gould) (Oceanitidae)	0.502
<i>Ninox novaeseelandiae</i> (Gmelin) (Strigidae)	0.169		
<i>Callaeas cinerea</i> (Gmelin) (Callaetidae)	0.190	<b>New Zealand forest bird fauna (species pool = 46)</b>	
<i>Hemiphaga novaeseelandiae</i> (Gmelin) (Columbidae)	0.210	<i>Strigops habroptilus</i> Gray (Psittacidae)	0.030
<i>Porphyrio hochstetteri</i> (Meyer) (Rallidae)	0.229	<i>Apteryx owenii</i> Gould (Apterygidae)	0.126
<i>Xenicus gilviventris</i> Pelzeln (Acanthisittidae)	0.248	<i>Halcyon sancta</i> Vigors & Horsfield (Alcedinidae)	0.182
<i>Diomedea melanophrys</i> Temminck (Diomedidae)	0.266	<i>Chrysococcyx lucidus</i> (Gmelin) (Cuculidae)	0.235
<i>Circus approximans</i> Peale (Accipitridae)	0.282	<i>Callaeas wilsoni</i> (Bonaparte) (Callaeidae)	0.287
<i>Calidris tenuirostris</i> (Horsfield) (Scolopacidae)	0.297	<i>Ninox novaeseelandiae</i> (Gmelin) (Strigidae)	0.337
<i>Falco novaeseelandiae</i> Gmelin (Falconidae)	0.311	<i>Falco novaeseelandiae</i> Gmelin (Falconidae)	0.385
<i>Tachybaptus novaehollandiae</i> (Stephens) (Podicipedidae)	0.326	<i>Hemiphaga chathamensis</i> (Rothschild) (Columbidae)	0.432
<i>Phalacrocorax carbo</i> (Linnaeus) (Phalacrocoracidae)	0.338	<i>Porphyrio hochstetteri</i> (Meyer) (Rallidae)	0.477
<i>Gerygone igata</i> (Quoy & Gaimard) (Acanthizidae)	0.351	<i>Xenicus gilviventris</i> Pelzeln (Acanthisittidae)	0.521
<i>Procelsterna cerulea</i> (Bennett) (Laridae)	0.363		
<i>Bowdleria punctata</i> (Quoy & Gaimard) (Sylviidae)	0.375	<b>Waikato forest bird fauna (species pool = 24)</b>	
<i>Botaurus poiciloptilus</i> (Wagler) (Ardeidae)	0.387	<i>Philesternus rufusater</i> (Lesson) (Callaeidae)	0.029
<i>Sula dactylatra</i> Lesson (Sulidae)	0.399	<i>Apteryx australis</i> Shaw & Nodder (Apterygidae)	0.164
<i>Petroica australis</i> (Sparrman) (Eopsaltriidae)	0.410	<i>Halcyon sancta</i> Vigors & Horsfield (Alcedinidae)	0.237
<i>Anthus novaeseelandiae</i> (Gmelin) (Motacillidae)	0.420	<i>Chrysococcyx lucidus</i> (Gmelin) (Cuculidae)	0.306
<i>Platalea regia</i> Gould (Threskiornithidae)	0.431	<i>Cyaoramphus novaezealandiae</i> (Sparrman) (Psittacidae)	0.373
<i>Mohoua novaeseelandiae</i> (Gmelin) (Pachycephalidae)	0.441	<i>Ninox novaeseelandiae</i> (Gmelin) (Strigidae)	0.439
<i>Aptenodytes patagonicus</i> Miller (Spheniscidae)	0.451	<i>Falco novaeseelandiae</i> Gmelin (Falconidae)	0.502

**Table 9.** An analysis of the predictive power of indicator species subsets based on a retrospective analysis of changes in the New Zealand forest bird fauna over the last two millennia

	Indicator subsets			
	Random species <sup>a</sup>	Random species <sup>b</sup>	Cumulative PD <sup>c</sup>	Entire fauna
Faunas at 2000 BP				
Species richness	20	20	20	88
Species richness as proportion of that for entire fauna	0.23	0.23	0.23	1.00
PD	792	1382	1986	3487
PD as proportion of that for entire fauna	0.23	0.40	0.57	1.00
Loss over last two millennia				
Observed loss in species richness	9.6	8	9	42
Species richness loss as proportion of loss in entire fauna	0.23	0.19	0.21	1.00
Observed loss in PD	380	364	820	1257
PD loss as proportion of loss in entire fauna	0.30	0.29	0.65	1.00

<sup>a</sup>Mean of 1000 random draws of 20 species. <sup>b</sup>A single random draw of 20 species. <sup>c</sup>The subset of 20 species with the greatest cumulative PD.

Evolutionary and phylogenetic studies are an important component of the scientific contribution because they enable the understanding of scales of change and the interpretation of biota (Main, 1996). Phylogenetic relationships also provide a quantitative basis for

measurement of biodiversity and priority where the assets of interest are features and feature complementarity that confer option value. Cladistic analysis of phylogenetic pattern provides a predictive means of modelling the underlying distribution of features

**Table 10.** An analysis of the predictive power of indicator species subsets based on a retrospective analysis of changes in the Waikato forest bird fauna over the last two millennia

	Indicator subsets			Entire fauna
	Random species <sup>a</sup>	Random species <sup>b</sup>	Cumulative PD <sup>c</sup>	
Faunas at 2000 BP				
Species richness	15	15	15	49
Species richness as proportion of that for entire fauna	0.36	0.36	0.36	1.00
PD	855	1202	1664	2792
PD as proportion of that for entire fauna	0.36	0.43	0.60	1.00
Loss over last two millennia				
Observed loss in species richness	8.6	10	6	24
Species richness loss as proportion of loss in entire fauna	0.36	0.42	0.25	1.00
Observed loss in PD	490	456	917	1080
PD loss as proportion of loss in entire fauna	0.45	0.29	0.65	1.00

<sup>a</sup>Mean of 1000 random draws of 15 species. <sup>b</sup>A single random draw of 15 species. <sup>c</sup>The subset of 15 species with the greatest cumulative PD.

among taxa (Farris, 1979; Faith, 1992a) and is the basis for the Phylogenetic Diversity (PD) measure first proposed by Faith (1992a) and central to the present paper.

As alluded to in the introduction, PD has not yet gained prominence in conservation and has received even less application in the general area of resource management. This paper deals explicitly with illustrating the range of applications to which phylogenetic diversity can be applied. Case studies on birds are chosen as the vehicle for communication because of the high public interest in this component of biodiversity, the prominence of birds in conservation activities globally and, as a consequence, the extent and quality of the available data.

PD as an approach to biodiversity measurement is not advocated at the exclusion of all others. Nevertheless, there are pragmatic advantages in a single currency of biodiversity measurement across a range of resource management situations. The recognition that the importance of biodiversity lies in its option value, and that this option value can be predicted from phylogenies, is therefore of critical importance as it provides the quantitative framework for potentially working in a single currency across taxonomic groups and ecosystems.

The DNA–DNA hybridization tree of Sibley & Ahlquist (1990), that provided the foundation for the present work, is not strictly cladistic in that units of measurement were not features. Nonetheless the application of the PD methodology is justified as DNA–DNA hybridization provides estimates of pattern of divergences (relative positions of the nodes in the cladogram) and genomic similarity (relative

amounts of phylogenetic divergence). The merits or otherwise of DNA–DNA hybridization as an approach is estimation of phylogeny, and the specific methods used by Sibley & Ahlquist (1990) in constructing their phylogenetic trees, have been well canvassed in the systematic and ornithological literature and will not be repeated here. Faith (1992a,b, 1994) has demonstrated the utility of PD across a range of data types, from robust phylogenies based on large sets of DNA sequences to taxonomic hierarchies where relative amounts of divergence are estimated by taxonomic level. However, the advantage of PD over simple species richness estimates in detecting variation in biodiversity option value declines along the gradient from robust phylogenies to taxonomic hierarchies based on taxonomic level. The use of simplified taxonomic hierarchies as approximations of phylogeny can lead to erroneous conclusions on the value of PD as a biodiversity measure.

Our understanding of the phylogeny of a particular group is not a static bit of information. Rather, estimates of relationships are altered or refined as new comparative data become available. In some cases, this results from the addition of new characters to a previously analysed dataset. In others, different datasets are analysed separately to yield results that contrast to varying degrees. Thus, indices of phylogenetic diversity, like estimates of phylogeny, are conditional on particular samples of characters or measurements of divergence. The prospect of improved data quality in the future should be no justification for failure to adopt PD and like methodologies and continued decision-making in a data free environment.

The phylogenetic tree, and associated distance matrix, developed in the present work from integration of the DNA–DNA hybridization tree of Sibley & Ahlquist (1990) and numerous cladistic-based phylogenetic hypotheses, has enabled for the first time quantitative analyses of avian phylogenetic diversity at any spatial scale. In one case study presented here, this phylogenetic tree provided the PD framework for monitoring compositional changes in avian faunas at country (New Zealand) and regional (Waikato) scales within a global context. In another, it provided the framework for the objective selection of indicator species sets. Both case studies illustrate the application of PD to *State of the Environment* reporting, where the objective is monitoring changes in option value. Indicator species have potential application across a broad range of environmental issues when resources prevent monitoring of entire communities.

Building on concepts introduced by Witting *et al.* (1994), an approach to the integration of PD with information on species' survivorship expectations was developed as a basis for prioritization among conservation projects. Its application was demonstrated in a case study on threatened New Zealand forest birds, where phylogenetic diversity estimates were combined with information on expected gains in species' survivorship under current management. While there is a growing recognition of distinctiveness as a key criterion in conservation decision-making, there is considerable scope for quantitative evaluation of this attribute in setting and auditing achievement (*sensu* Stephens, 1999) in respect of maintenance of biodiversity option values.

In its basic form as used in the above case studies, PD will over a large series of samples be correlated with species richness in an approximately linear fashion. Thus, PD will vary at a particular level of richness depending on the dispersion of the species across the phylogenetic tree, but the range of possible PD values converges as richness approaches that of the entire species pool. Despite the linear correlation, PD values can vary substantially between communities of similar richness and therefore provides a useful complement to richness in differentiating biodiversity value of communities. PD values will vary temporally at a locality only with the loss or gain of species, resulting, respectively, from extinctions or re-establishments. The extension to the PD methodology that enables incorporation of abundance data, developed in this paper, greatly increases the utility of PD in monitoring compositional changes in communities. In  $\Delta$ nPD we have a measure that is sensitive to changes in the relative abundance of individuals among species that differ in option value. In the context of *State of the Environment* reporting, the utility of  $\Delta$ nPD was demon-

strated by the use of extent of habitat loss as a surrogate for changes in abundance in Waikato forest bird fauna over the last two millennia. In the context of ecosystem management,  $\Delta$ nPD was applied to 5-minute bird counts under three contrasting land-use regimes in New Zealand to illustrate utility in monitoring community response to management.

Thus, for biological community data (species-by-sample abundance matrices) we have in  $\Delta$ nPD an index that encapsulates information not only about the distribution of abundances among species, but also about the amount of novel features contributed by the species in each sample. In the special case where the data consist only of presence (or presence/absence) information,  $\Delta$ nPD collapses to the PD statistic. The utility of these indices, as with any index, is dependent on its robustness and sensitivity. PD is well-grounded in cladistic theory. The case studies presented in the present paper demonstrate that PD and  $\Delta$ nPD are informative about option values in a diverse range of situations of interest to resource managers. When based on a well-resolved phylogeny, the information conferred offers a considerable advance of species richness as a biodiversity index.

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## APPENDIX

List of phylogenetic trees sourced from the literature that were considered in the construction of within-Order supertrees (see text for further details). All supertrees were constrained to comply with suprafamily divergence patterns indicated by the DNA–DNA hybridization experiments of Sibley and Ahlquist (1990). Nomenclature and sequence of presentation for ordinal taxa follows that of Sibley *et al.* (1988), Sibley and Ahlquist (1990) and Sibley and Monroe (1990).

Order	Nature of primary data from which trees were constructed	Data sources
Struthioniformes	DNA–DNA hybridization	Sibley and Ahlquist (1981)
	Morphology	Cracraft (1974), Bledsoe (1988), Lee, Feinstein and Cracraft (1997)
	12S rDNA	Cooper <i>et al.</i> (1992), Cooper and Cooper (1995), Cooper (1997)
	16S rDNA + 12S rDNA + COI + COII + cytochrome b + tRNA sequences	Lee, Feinstein and Cracraft (1997)
	16S rDNA + 12S rDNA + COI + COII + cytochrome- <i>b</i> + tDNA sequences + morphology 12S rDNA + t rDNA-valine + 16S rDNA sequences	Lee, Feinstein and Cracraft (1997) van Tuinen, Sibley and Hedges (1998)
Tinamiformes		
Craciformes		
Galliformes	Cytochrome- <i>b</i> sequences	Ellsworth, Honcutt and Silvy (1996)
	Morphology	Johnsgard (1988)
	12S rDNA sequences	Mindell <i>et al.</i> (1997)
Anseriformes	Cytochrome- <i>b</i> sequences	Sraml <i>et al.</i> (1996)
	Cytochrome- <i>b</i> + ND2 sequences	Johnson and Sorenson (1998)
	DNA-DNA hybridization	Madsen, McHugh and de Kloet (1988)
	Morphology 12S rDNA sequences	Livezey (1986, 1989, 1991, 1995a,b, 1996a,b,c, 1997a,b,c) Mindell <i>et al.</i> (1997)
Turniciformes		
Piciformes	Cytochrome- <i>b</i> sequences	Lanyon and Hall (1994), Moore and DeFilippis (1997)
Galbuliformes		
Bucerotiformes		
Upupiformes		
Trogoniformes	DNA–DNA hybridization	Bleiweiss, Kirsch and Matheus (1994, 1977)
Coraciiformes		
Cuculiformes	Behaviour + ecology	Hughes (1996)
	Morphology	Seibel (1988), Hughes (1996)
	12S rDNA sequences	Mindell <i>et al.</i> (1997)
Psittaciformes	Cytochrome- <i>b</i> sequences	Leeton <i>et al.</i> (1994)
	Morphology	Holyoak (1973), Smith (1975)
	Protein electrophoresis	Adams <i>et al.</i> (1984), Christidis <i>et al.</i> (1991), Triggs and Daugherty (1996)
	12S rRNA	Brown and Toft (1999)
Apodiformes	Cytochrome- <i>b</i> sequences	Lee <i>et al.</i> (1996)

Trochiliformes		
Musophagiformes		
Strigiformes	12S rDNA sequences	Mindell <i>et al.</i> (1997)
Columbiformes		
Gruiformes	Cytochrome- <i>b</i> sequences	Krajewski and Fetzner (1994), Krajewski and King (1996), Moore and DeFilippis (1997), Trewick (1997)
	DNA-DNA hybridization	Krajewski (1989), Krajewski and Dickerman (1990), Houde, Sheldon and Kreitman (1995)
	Morphology	Cracraft (1973), Houde (1994), Livezey (1998)
	12S rDNA sequences	Houde <i>et al.</i> (1997), Trewick (1997)
Ciconiiformes	Behaviour + life history	Paterson, Wallis and Gray (1995)
	Cytochrome- <i>b</i> sequences	Awise, Nelson and Sibley (1994), Seibold and Helbig (1995), Wink (1995), Nunn <i>et al.</i> (1996), Wink, Heidrich and Fentzloff (1996), Friesen and Anderson (1997), Robertson and Nunn (1997)
	DNA-DNA hybridization	McCracken and Sheldon (1998)
	Morphology	Schnell (1970), Strauch (1978), Mickevich and Parenti (1980), Cracraft (1985), Siegel-Causey (1988), Björklund (1994), Griffiths (1994), Hedge and Sibley (1994), Chu (1998), McCracken and Sheldon (1998), Griffiths (1999)
	Protein electrophoresis	Dittmann, Zink and Gerwin (1989), Hackett (1989), Olsen, Marshall and Gaal (1989), Christian, Christidis and Schodde (1992), Paterson, Wallis and Gray (1995)
	Cytochrome- <i>b</i> sequences + protein electrophoresis	Friesen, Baker and Piatt (1996)
	Cytochrome- <i>b</i> + 12S sequences	Cohen <i>et al.</i> (1997)
	mtDNA restriction fragments	Dittmann and Zink (1991), Braun and Brumfield (1998)
	12S rDNA sequences	Paterson, Wallis and Gray (1995), Mindell <i>et al.</i> (1997)
	12S rDNA and 16S rDNA sequences	Hedge and Sibley (1994)
	12S rDNA + mtCOI sequences	Mindell <i>et al.</i> (1997)
	12S rDNA + protein electrophoresis + behaviour + life history	Paterson, Gray and Wallis (1993), Paterson, Wallis and Gray (1995)
Passeriformes	Cytochrome- <i>b</i> sequences	Helm-Bychowski and Cracraft (1993), Lanyon and Omland (1994), Christidis, Leeton and Westweman (1996), Moore and DeFilippis (1997), Cibois and Pasquet (1999), Sheldon, Whittingham and Winkler (1999)
	DNA-DNA hybridization	Sibley, Williams and Ahlquist (1982), Sheldon and Winkler (1993), Sheldon and Gill (1996)
	Cytochrome- <i>b</i> sequences + DNA-DNA hybridization	Sheldon, Whittingham and Winkler (1999)
	Morphology	Raikow (1994)
	Protein electrophoresis	Christidis and Schodde (1991, 1992)
	12S rDNA sequences	Cooper (1994), Cooper and Cooper (1995), Mindell <i>et al.</i> (1997)
	16S rDNA sequences	Sturmbauer <i>et al.</i> (1998)