Can taxonomic richness be used as a surrogate for phylogenetic distinctness indices for ranking areas for conservation?

M. Pérez–Losada & K. A. Crandall

Abstract

Can taxonomic richness be used as a surrogate for phylogenetic distinctness indices for ranking areas for conservation?— Several methods have been proposed for evaluating area conservation priorities. Here the performance of traditional approaches (taxonomic richness) versus newer methods of phylogenetic distinctness is compared using the results and data from three different molecular studies: crayfish from the central United States and Australia, and Aeglidae freshwater crabs from Chile. To a large extent rankings based on species and genus richness agree with rankings based on taxonomic, phylogenetic and genetic diversity, thus suggesting that taxonomic richness methods may be used as a surrogate for the phylogenetic distinctness methods for the purpose of prioritizing reserve areas for conservation.

Key words: Conservation priorities, Phylogenetic distinctness, Taxonomic richness.

Resumen

¿Puede utilizarse la riqueza taxonómica como un indicativo de diferenciación filogenética para evaluar áreas de conservación?— Se han propuesto varios métodos para evaluar prioridades de conservación de áreas. En este trabajo se compara el funcionamiento de métodos tradicionales (riqueza taxonómica) frente a métodos más recientes de diferenciación filogenética utilizando los resultados y datos de tres estudios moleculares diferentes: cangrejos de agua dulce de los estados centrales de Estados Unidos y Australia, y cangrejos de agua dulce Aeglidae de Chile. En gran medida los ordenamientos basados en riqueza específica y genérica coinciden con los basados en diversidad taxonómica, filogenética y genética, sugiriendo por lo tanto que la riqueza taxonómica puede ser utilizada como un indicativo de diferenciación filogenética con el objetivo de priorizar reservas para su conservación.

Palabras clave: Prioridades de conservación, Diferenciación filogenética, Riqueza taxonómica.

Marcos Pérez–Losada & Keith A. Crandall, Dept. of Integrative Biology, 401 Widtsoe Building, Brigham Young Univ., Provo UT 84602–5181, U. S. A.

Corresponding author: Dr. M. Pérez–Losada. E–mail: mp323@email.byu.edu

Introduction

The most effective way of preserving biodiversity is by maintaining self–sustaining populations of native species in their natural ecosystems (RODRIGUES & GASTON, 2002). This often requires the designation of nature reserves, areas where conservation of biodiversity is a priority over other forms of land use. However, because maintaining the integrity of these areas often imposes restrictions to other economically and/or socially important human activities, there will always be limitations to the total amount of land that can be set aside for conservation purposes (VANE–WRIGHT et al., 1991; FAITH, 1992).

Methods for ranking areas for the selection of reserve networks have been proposed as a response to these concerns. Traditional approaches such as species and genus richness (MAY, 1981; BROWN, 1988; SCHLUTER & RICKLEFS, 1993), assume that all units are taxonomically equivalent, and assign the same value for conservation. But is it appropriate to regard all species as equal in this matter? If faced with saving either a species not closely related to any other extant taxa (such as the tuataras or *Welwitshia*) or a species with many close relatives (such as species of grass snake and *Taraxacum*), it would look more reasonable to keep the former because its extinction would represent a much greater loss of evolutionary history and genetic diversity. Taxonomically distinct species and the places where they occur, should therefore be given priority in the allocation of conservation resources. This can be achieved by using a currency of biological diversity which takes the phylogenetic relationships between species (hence evolutionary history) into account. Over the last ten years several methods have been proposed for measuring taxonomic distinctness using phylogenetic information, and presently they are mostly applied to molecular data (see HUMPHRIES et al., 1995 and CROZIER, 1997 and references therein; and MORITZ & FAITH, 1998; OWENS & BENNETT, 1999; POSADAS et al., 2001). Phylogenetic distinctness is defined quantitatively either by reference to the topology (VANE–WRIGHT et al., 1991; NIXON & WHEELER, 1992; POSADAS et al., 2001), genetic divergence (SOLOW et al., 1993; WEITZMAN, 1992), or both (CROZIER, 1992; FAITH, 1992, 1994).

In spite of the appeal of phylogenetic methods, several studies have recently been published that suggest that traditional indices such as taxonomic richness could be a good surrogate for phylogeny–based methods in ranking and prioritizing areas for conservation (WILLIAMS & HUMPHRIES, 1996; CRANDALL, 1998; HACKER et al., 1998; WHITING et al., 2000; POLASKY et al., 2001; PÉREZ–LOSADA et al., 2002; RODRIGUES & GASTON, 2002). In this study this question is addressed by comparing different biodiversity indices using data from three studies on freshwater invertebrates (CRANDALL, 1998; WHITING et al., 2000; PÉREZ–LOSADA et al., 2002).

Material and methods

Results from three different studies on freshwater macroinvertebrates including crayfish from the Ozark Plateaus (CRANDALL, 1998) and Australia (WHITING et al., 2000), and crabs of the family Aeglidae from Chile (PÉREZ–LOSADA et al., 2002) are compared. The Ozark Plateau is located in the central United States and encompasses much of southern Missouri and northern Arkansas. It has been subdivided into six regions characterized by the major river drainages within each as Neosho, White, Black, Southeast, Mississippi, and Missouri. Australia has been subdivided in forty–eight areas according to the Interim Biogeographic Regionalisation for Australia (IBRA) representing unique habitats and ecosystems (THACKWAY & CRESSWELL, 1995). Finally, temperate Chile encompasses twenty different main basins which have been divided in six hydrographic regions, named here with letters from A to F (see table 1).

These studies have been chosen for several reasons: 1) the studied organisms represent different taxonomic levels (populations, species, and genera); 2) the areas of concern have been extensively studied and represent three well-known regions with very different ecological, faunistic, and geological characteristics; 3) all of them use different traditional and molecular phylogenetic indices for assessing conservation priorities and provide adequate information for estimating new indices if necessary; 4) the phylogenetic trees (fig. 1) representing the relationships among the studied taxa are fairly well supported and are based on different phylogenetic approaches (maximum parsimony, minimum evolution, and maximum likelihood) that make different assumptions about the evolutionary process.

In the previous studies phylogenetic assessments of conservation priorities were performed using two distinct approaches: the topological dependent methods of taxonomic diversity (TD; VANE–WRIGHT et al., 1991), and the distance and branch length dependent methods of genetic diversity (GD; CROZIER, 1992) and phylogenetic diversity (PD; FAITH, 1992), respectively. Topology dependent methods rely on a rooted phylogeny and reflect the branching order and, therefore, rank those organisms that evolved earliest with the highest priority regardless of divergence between species (NIXON & WHEELER, 1992; POSADAS et al., 2001). Distance or branch length dependent methods sum the branch lengths to derive a phylogenetic diversity for an organism and strive to represent the genetic diversity or divergence between each organism (FAITH, 1994; KRAJEWSKI, 1994). Estimates of species and generic phylogenetic diversity (S.PD and G.PD, respectively), and generic genetic diversity (G.GD) were separately calculated for the Australian IBRA areas. Non–phylogenetic methods as species (SR) and genus (GR) richness (total number of species presented in each area) were also estimated.

Table 1. Ozark (A), Australian (B), and Chilean (C) area ranks for different indices and complimentarity analysis. For Australia, only the twelve areas representing most of the top ten rankings are shown. Species richness (SR), genus richness (GR), taxonomic diversity (TD), phylogenetic diversity (PD), species phylogenetic diversity (S.PD), generic phylogenetic diversity (G.PD), and generic genetic diversity (G.GD) values are also indicated. Australian areas: SEH. South Eastern Highlands; WSW. West and South West; WOO. Woolnorth; VM. Victorian Midlands; SEQ. South Eastern Queensland; NNC. NSW North Coast; NCP. Naracoorte Coastal Plain; SCP. South East Coastal Plain; VVP. Victorian Volcanic Plain; SEC. South East Corner; WAR. Warren; NSS: NSW South Western Slopes. Chilean hydrographic areas: A. Rivers of snowy and pluvious regimen; B. Rivers of snowy regimen with torrential draining; C. Rivers with snowy regimen and fast flood; D. Transition rivers; E. Rivers of constant flow and light slope; F. Patagonian rivers. n. a. Data not available.

Tabla 1. Clasificación de las áreas Ozark (A), Australia (B) y Chile (C) para diferentes índices y análisis de complementaridad. Para Australia, solamente se muestran las doce áreas más representadas en los diez primeros puestos. Se indican también los valores de riqueza específica (SR), riqueza genérica (GR), diversidad taxonómica (TD), diversidad filogenética (PD), diversidad filogenética específica (S.PD), diversidad filogenética genérica (G.PD) y diversidad genética genérica (G.GD). Áreas australianas: SEH. South Eastern Highlands; WSW. West y South West; WOO. Woolnorth; VM. Victorian Midlands; SEQ. South Eastern Queensland; NNC. NSW North Coast; NCP. Naracoorte Coastal Plain; SCP. South East Coastal Plain; VVP. Victorian Volcanic Plain; SEC. South East Corner; WAR. Warren; NSS. NSW South Western Slopes. Áreas hidrográficas chilenas: A. Ríos de régimen ligado a las nieves y lluvias; B. Ríos de régimen ligado a las nieves y con lluvias torrenciales; C. Ríos de régimen ligado a las nieves y con crecidas rápidas; D. Ríos de transición; E. Ríos con caudal constante y desnivel poco pronunciado; F. Ríos de Patagonia. n. a. Datos no disponibles.

A. Ozark areas

	Neosho	White	Black	Southeast	Mississippi	Missouri
SR	5	9	8	3	8	2
TD	8.0	18.5	13.0	3.4	15.5	2.2
PD	73	114	117	48	159	18
SR Rank	4	1	2–3	5	2–3	6
TD Rank	4	1	3	5	2	6
PD Rank	4	3	2	5	1	6
Complementarity analysis						
SR	2	9	4	2	7	1
TD	4.3	18.5	4.0	2.2	14.3	1.0
PD	57	108	89	7	159	0
SR Rank	4–5	1	3	4–5	2	6
TD Rank	3	1	4	5	2	6
PD Rank	4	2	3	5	1	6

B. Australian areas

	SEH	WSW	WOO	VM	SEQ	NNC	NCP	SCP	VVP	SEC	WAR	NSS
SR	26	16	14	9	15	17	5	15	8	13	9	3
GR	4	4	4	5	3	3	5	3	4	3	2	3
S.PD	66.4	78.0	46.9	25.7	42.4	31.4	15.1	39.3	23.0	25.9	37.1	8.9
G.PD	12.5	15.2	15.2	15.1	8.8	8.8	15.1	7.2	12.2	6.8	7.9	8.9
G.GD	16.2	17.8	17.8	19.5	12.2	12.2	19.5	10.8	15.9	7.1	6.4	11.4
SR Rank	1	3	6	9–10	4–5	2	>10	4–5	>10	7	9–10	>10
GR Rank	3–6	3–6	3–6	1–2	≥7	≥7	1–2	≥7	3-6	≥7	≥10	=7
S.PD Rank	2	1	3	10	4	8	>10	5	>10	9	6	>10
G.PD Rank	5	1–2	1–2	3–4	≥10	≥10	3–4	>10	6	>10	>10	9
G.GD Rank	5	3–4	3–4	1–2	7–8	7–8	1–2	10	6	>10	>10	9

Table 1. (Cont.)

	SEH	WSW	WOO	VM	SEQ	NNC	NCP	SCP	VVP	SEC	WAR	NSS
Complementarity analysis												
SR	26	15	3	0	11	16	0	0	5	9	9	0
GR	0	2	2	5	1	1	5	0	0	0	1	0
S.PD	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
G.PD	0	15.2	15.2	8.9	2.5	2.5	8.9	0	8.9	0	2.6	0
G.GD	0	9.7	9.7	19.5	4.2	4.2	19.5	0	0	0	1.0	0
SR Rank	1	3	9	≥10	4	2	≥10	10	8	5–6	5–6	≥10
GR Rank	>10	3–6	3–6	1–2	7–10	7–10	1–2	>10	>10	>10	7–10	>10
S.PD Rank	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
G.PD Rank	≥10	1–2	1–2	3–5	8–9	8–9	3–5	≥10	3–5	≥10	6–7	≥10
G.GD Rank	>10	3–6	3–6	1–2	7–8	7–8	1–2	>10	>10	>10	9–10	>10

C. Chilean hydrographic areas

	A	B	C	D	E	F
SR	1	4	6	9	7	4
TD	8.0	12.6	11.1	17.9	13.3	8.7
PD	4.65	12.58	9.28	16.56	13.84	7.12
GD	2.55	8.09	6.99	11.88	9.76	5.12
SR Rank	6	4–5	3	1	2	4–5
TD Rank	6	3	4	1	2	5
PD Rank	6	3	4	1	2	5
GD Rank	6	3	4	1	2	5
Complementarity analysis						
SR	1	3	2	9	3	1
TD	8.0	10.6	5.1	17.9	5.6	2.0
PD	4.65	10.52	4.16	16.56	5.72	1.63
GD	2.55	6.58	3.17	11.88	4.29	1.37
SR Rank	5–6	2–3	4	1	2–3	5–6
TD Rank	3	2	5	1	4	6
PD Rank	4	2	5	1	3	6
GD Rank	5	2	4	1	3	6

Fig. 1. De izquierda a derecha: 1. Árbol de máxima parsimonia obtenido a partir de la secuenciación del ADNmt 16S de especies de cangrejos de agua dulce procedentes de Ozark Plateaus estudiadas por CRANDALL (1998). Los números sobre las ramas del árbol indican el número de cambios no ambiguos a lo largo de cada rama. 2. Árbol de evolución mínima basado en la secuenciación del ADNmt 16S de cangrejos de agua de Australia según WHITING et al. (2000). 3. Árbol de máxima verosimilitud basado en los genes del ADNmt 12S, 16S, COI y COII de los cangrejos de agua dulce Aeglidae de Chile (PÉREZ–LOSADA et al., 2002). Bajo las ramas se indican los valores iniciales de ceba (valores "bootstrap") basados en 200 (árbol 1), 1.000 (árbol 2) y 100 (árbol 3) réplicas.
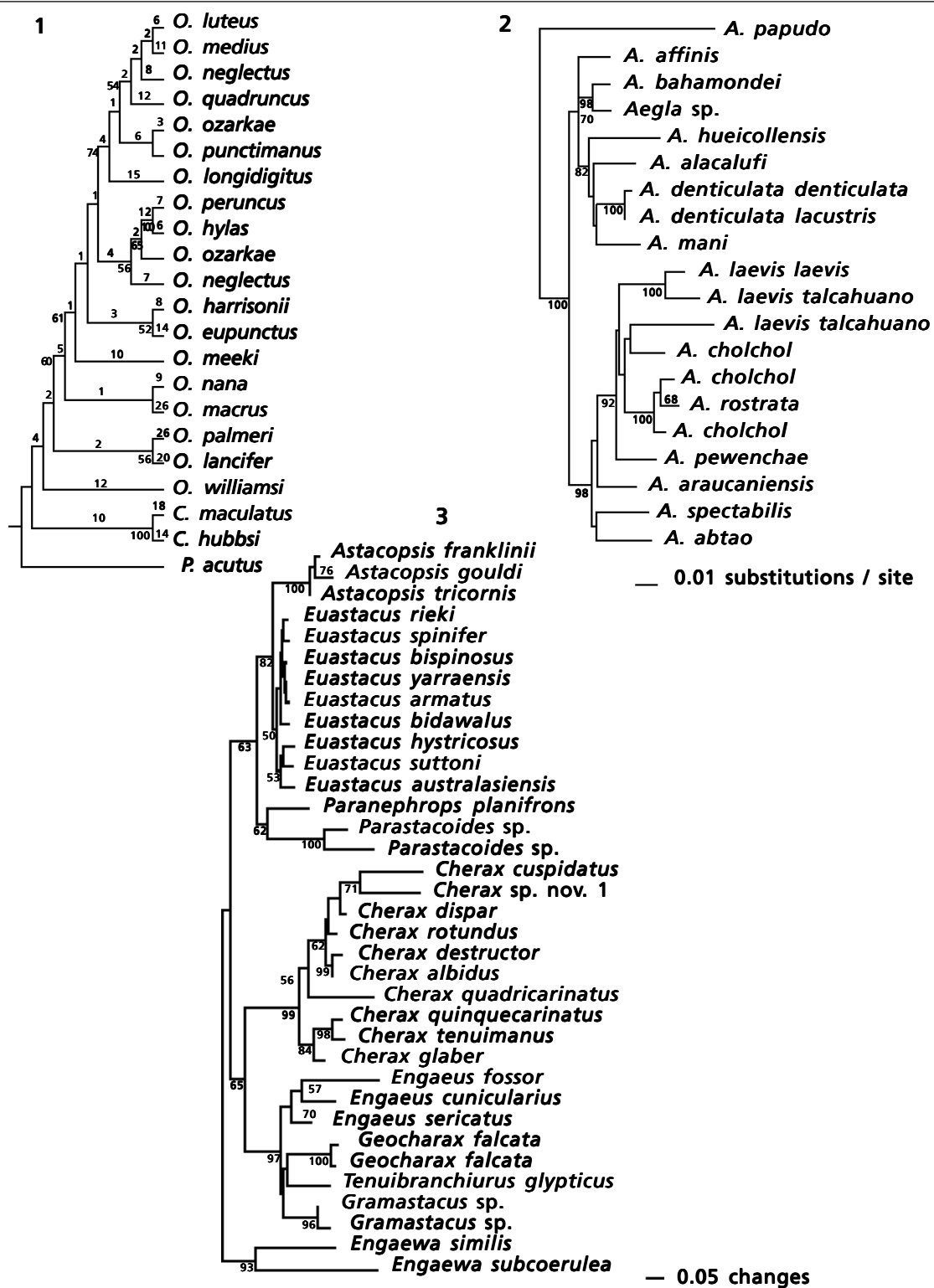
1

- O. luteus
- O. medius
- O. neglectus
- O. quadruncus
- O. ozarkae
- O. punctimanus
- O. longidigitus
- O. peruncus
- O. hylas
- O. ozarkae
- O. neglectus
- O. harrisonii
- O. eupunctus
- O. meeki
- O. nana
- O. macrus
- O. palmeri
- O. lancifer
- O. williamsi
- C. maculatus
- C. hubbsi
- P. acutus

2

- A. papudo
- A. affinis
- A. bahamondei
- Aegla sp.
- A. hueicollensis
- A. alacalufi
- A. denticulata denticulata
- A. denticulata lacustris
- A. mani
- A. laevis laevis
- A. laevis talcahuano
- A. laevis talcahuano
- A. cholchol
- A. cholchol
- A. rostrata
- A. cholchol
- A. pewenchae
- A. araucaniensis
- A. spectabilis
- A. abtao

— 0.01 substitutions / site

3

- Astacopsis franklinii
- Astacopsis gouldi
- Astacopsis tricornis
- Euastacus rieki
- Euastacus spinifer
- Euastacus bispinosus
- Euastacus yarraensis
- Euastacus armatus
- Euastacus bidawalus
- Euastacus hystricosus
- Euastacus suttoni
- Euastacus australasiensis
- Paranephrops planifrons
- Parastacoides sp.
- Parastacoides sp.
- Cherax cuspidatus
- Cherax sp. nov. 1
- Cherax dispar
- Cherax rotundus
- Cherax destructor
- Cherax albidus
- Cherax quadricarinatus
- Cherax quinquecarinatus
- Cherax tenuimanus
- Cherax glaber
- Engaeus fossor
- Engaeus cunicularius
- Engaeus sericatus
- Geocharax falcata
- Geocharax falcata
- Tenuibranchiurus glypticus
- Gramastacus sp.
- Gramastacus sp.
- Engaewa similis
- Engaewa subcoerulea

— 0.05 changes

Fig. 1. From left to right: 1. Maximum parsimony tree inferred from 16S mtDNA sequence data for the crayfish species from the Ozark Plateaus studied by CRANDALL (1998). Numbers above branches indicate the number of unambiguous changes along that branch. 2. Minimum evolution tree based on 16S mtDNA sequence data for the crayfish from Australia in WHITING et al. (2000). 3. Maximum likelihood tree based on 12S, 16S, COI, and COII mtDNA genes for the freshwater crabs Aeglidae from Chile (PÉREZ–LOSADA et al., 2002). Bootstrap values based on 200 (tree 1), 1000 (tree 2), and 100 (tree 3) replications are indicated below branches.

Because not all of these indices were estimated by the previous authors in their studies, some phylogenetic indices were calculated here for every area using information on taxa geographical distributions and phylogenetic relationships.

For conservation purposes it is important to identify areas that represent similar species richness thereby eliminating redundancy. Moreover, ranking areas according to their faunistic complementarity may alter the initial ordination based on non-complementarity information. In this study, we have therefore compared the resulted rankings from both phylogenetic and non–phylogenetic methods performed under both non–complementarity and complementarity analyses using the Spearman rank correlation coefficient.

Results and discussion

Phylogenetic and non–phylogenetic indices, as well as the area rankings derived from them, are shown in table 1 for the Ozark Plateaus, the top ten ranking Australian IBRA areas, and the Chilean hydrographic regions. Phylogenetic and non–phylogenetic indices showed significant positively correlated rankings ($P < 0.001$) within the Ozark (four comparisons) and the Chilean regions (six comparisons) for both the non–complementarity (initial ranks) and the complementarity analyses (Spearman rank correlation $r_s = 0.71 - 0.99$). All of these comparisons remained significant at $P < 0.01$ after sequential Bonferroni correction. Within the forty–eight IBRA Australian regions, there was also strong positive correlation between the rankings based on the number of genera per area (GR) and the generic PD and GD, as well as between the species richness (SR) and the species PD for the non–complementarity and the complementarity analyses (Spearman rank correlations $r_s = 0.76 - 0.99$, $P < 0.001$). All of these comparisons remained significant at $P < 0.01$ after sequential Bonferroni correction. But when the species–based methods are compared directly with the genus–based methods, there are strong disparities in the resulting conservation rankings ($r_s < 0.001$). WILLIAMS et al. (1994), BALMFORD et al. (1996), and RICOTTA et al. (2002) addressed the question of whether it is reasonable to use higher taxon richness as a surrogate for species richness in evaluating conservation priorities. They found that there is generally a good correlation between genus richness and species richness, but this correlation decreases as the number of species increases (BALMFORD et al., 1996). The results of this study show that the disparity between genus and species richness occurs in those areas with the greatest species richness (SEH, NNC, SEQ, SCP, and SEC).

All of the three compared studies show that there is little difference between the traditional biodiversity measures and the newer phylogenetic approaches, estimated from maximum parsimony, minimum evolution or maximum likelihood trees either performed under non–complementarity or complementarity analyses. The largest deviations between taxon richness and phylogeny–based methods were the WAR and the NNC areas from the Australian IBRA regionalisation, and region B from the Chilean hydrographic regions. Areas WAR and NNC have nine and seventeen species, respectively, but species PD of 37.1 and 31.4, respectively. Region B has only four species, but a PD of 12.58 (see table 1B, 1C). This reflects the fact that the species in areas WAR and B represent more phylogenetically distinct taxa than those found in other regions.

Similar results were found by WILLIAMS & HUMPHRIES (1996), HACKER et al. (1998), POLASKY et al. (2001), and RODRIGUES & GASTON (2002) when comparing taxon richness versus taxonomic diversity and phylogenetic diversity (with branch lengths estimated assuming a molecular clock) using bird species from North America and African primates. They concluded that the congruence of methods is certainly not perfect, but when these methods are used for ranking areas for conservation priorities the general ranks tend to be the same. Therefore, our results also support the assertion that taxon richness is a good surrogate for phylogenetic diversity. It has been graphically illustrated that either measure based on the number of branching nodes (e.g. taxonomic diversity) or branch lengths (e.g. phylogenetic diversity) increases as taxa are added and are positively correlated to taxonomic richness (NEE & MAY, 1997; POLASKY et al., 2001; RODRIGUES & GASTON, 2002).

However, extreme taxon richness is not the only way in which an area could make a large contribution to phylogenetic diversity. Scenarios can be proposed where both measures lead to different area rankings. If the tree is unbalanced with some of the branches being ramified (e.g. recent speciation process) while others correspond to older monophyletic taxa, and if there is a spatial segregation between sites where these two types of branches occur (e.g. due to a vicariance event), one would expect that taxonomic richness indices will tend to select sites with many closely related species while phylogenetic indices will tend to select sites with more distinct taxa. For example in the minimum evolution tree depicted in fig. 1 (2nd tree), an area represented by the twelve species in the top clade (*Atacopsis* and *Euastacus*) would have a PD of 1.0, while an area represented by the 3 species in its sister clade (*Paranephrops* and *Parastacoides*) would have a PD of 1.22. These two areas would clearly rank different for both indices. A parallel situation may also occur if the study area includes sites with marked differences in taxonomic structure (GASTON, 2000). The radiation of lemurs in Madagascar could be an example (HACKER et al., 1998).

Therefore, the use of phylogenetic–based information indices could help to assist decisions concerning conservation priorities because they consider the evolutionary component of biodiversity and allow identification of those areas that will ensure the preservation of evolutionary potential and phylogenetically different species (BROOKS et al., 1992). Indeed, as preserving genetic diversity is often a goal in conservation biology (TEMPLETON, 1991; CROZIER, 1992), it seems pertinent to include some measure of genetic distinctness into a weighting scheme for habitat preservation (CRANDALL, 1998). However, it has been suggested that no single measure is adequate for complete evaluation of biodiversity, so it seems more adequate to integrate different approaches to yield a broad perspective on conservation priorities (POSADAS et al., 2001). Either combining different biodiversity indices or developing measures that integrate ecological considerations of abundance, endemicity, and geographic distribution with the evolutionary history of the taxa as both topology and genetic divergence, will allow for a more accurate ranking of areas for conservation priorities. In this latter sense new biodiversity measures such as the "taxonomic endemicity standardized weight" index proposed by POSADAS et al. (2001) appears to be a promising rationale. A modification of this index to include genetic distinctiveness as genetic distances into the equation would be desirable.

Recommendations

Given unlimited resources, the optimal way to compute conservation rankings is to use every species in reconstructing a phylogeny. In this way, the PD for every species present in an area could be summed up, resulting in an accurate representation of both species richness and genetic diversity. One of the major functional constraints of phylogenetic diversity measures is sampling (FAITH, 1992). Branch lengths are dependent on sister taxa, therefore if sampling is incomplete the resulting conservation priorities will vary greatly depending on the taxa chosen. If there is not an option of complete sampling a method must be chosen that best represents the available information. The subtle differences between the traditional and phylogenetic methods does not seem to be sufficient to warrant the added expense of obtaining sequence data for every taxon. However, phylogenetic distinctness measures appear to be very useful in providing information concerning which genera or species are the most genetically distinct. When one area or taxon must be chosen over another, information from PD values are extremely useful. Therefore, in ranking areas for conservation, we suggest that in cases of limited resources a species count be taken first, and then sufficient sequence data be obtained to compute phylogenetic diversity values.

Acknowledgements

References

BALMFORD, A., GREEN, M. J. B. & MURRAY, M. G., 1996. Using higher–taxon richness as a surrogate for species richness: I. Regional tests. *Proceedings of the Royal Society of London*, 263: 1,267–1,274.

BROOKS, D. R., MAYDEN, R. L. & MACLENNAN, D. A., 1992. Phylogeny and biodiversity: conserving our evolutionary legacy. *Trends in Ecology and Systematics*, 7: 55–59.

BROWN, J. H., 1988. Species diversity. In: *Analytical biogeography*: 57–89 (A. A. Myers & P. S. Giller, Eds.). London, Chapman & Hall.

CRANDALL, K. A., 1998. Conservation phylogenetics of Ozark crayfishes: assigning priorities for aquatic habitat protection. *Biological Conservation*, 84: 107–117.

CROZIER, R. H., 1992. Genetic diversity and the agony of choice. *Biological Conservation*, 61: 11–15.

– 1997. Preserving the information content of species: genetic diversity, phylogeny, and conservation worth. *Annual Review of Ecology and Systematics*, 28: 243–268.

FAITH, D. P., 1992. Conservation evaluation and phylogenetic diversity. *Biological Conservation*, 61: 1–10.

– 1994. Genetic diversity and taxonomic priorities for conservation. *Biological Conservation*, 68: 69–74.

GASTON, K. J., 2000. Biodiversity: higher taxon richness. *Progress in Physical Geography*, 24: 117–127.

HACKER, J. E., COWLISHAW, G. & WILLIAMS, P. H., 1998. Patterns of African primate diversity and their evaluation for the selection of conservation areas. *Biological Conservation*, 84: 251–262.

HUMPHRIES, C. J., WILLIAMS, P. H. & VANE–WRIGHT, R. I., 1995. Measuring biodiversity value for conservation. *Annual Review of Ecology and Systematics*, 26: 93–111.

KRAJEWSKI, C., 1994. Phylogenetic measures of biodiversity: a comparison and critique. *Biological Conservation*, 69: 33–39.

MAY, R. M., 1981. Patterns in multiple species communities. In: *Theoretical ecology, 2nd edition*: 197–227 (R. M. May, Ed.). Sinauer Associates, Sunderland, Massachusetts.

MORITZ, G. & FAITH, D. P., 1998. Comparative phylogeography and the identification of ge-

netically divergent areas for conservation. *Molecular Ecology*, 7: 419–429.

NEE, S. & MAY, R. M., 1997. Extinction and the loss of evolutionary history. *Science*, 278: 692–694.

NIXON, K. C. & WHEELER, Q. D., 1992. Measures of phylogenetic diversity. In: *Extinction and phylogeny*: 216–234 (M. J. Novacek & Q. D. Wheleer, Eds.). Columbia University Press, New York.

OWENS, I. P. F. & BENNETT, P. M., 1999. Quantifying biodiversity: a phenotipic perspective. *Conservation Biology*, 14: 1,014–1,022.

PEREZ–LOSADA, M., JARA, C. G., BOND–BUCKUP, G. & CRANDALL, K. A., 2002. Conservation phylogenetics of Chilean freshwater crabs *Aegla* (Anomura, Aeglidae): assigning priorities for aquatic habitat protection. *Biological Conservation*, 105: 345–353.

POLASKY, S., CSUTI, B., VOSSLER, C. A. & MEYERS, S. M., 2001. A comparison of taxonomic distinctness versus richness as criteria for setting conservation priorities from North American birds. *Biological Conservation*, 97: 99–105.

POSADAS, P., MIRANDA ESQUIVEL, D. R. & CRISCI, J. V., 2001. Using phylogenetic diversity measures to set priorities in conservation: an example from southern South America. *Conservation Biology*, 15: 1325–1334.

RICOTTA, C., FERRARI, M. & AVENA, G., 2002. Using the scaling behaviour of higher taxonomic taxa for the assessment of species richness. *Biological Conservation*, 107: 131–133.

RODRIGUES, A. S. L. & GASTON, K. J., 2002. Maximising phylogenetic diversity in the selection of networks of conservation areas. *Biological Conservation*, 105: 103–111.

SCHLUTER, D. & RICKLEFS, R. E., 1993. Species diversity: an introduction to the problem. In: *Species diversity in ecological communities*: 1–10 (R. E. Ricklefs & D. Schluter, Eds.). Chicago University Press, Chicago.

SOLOW, A., POLASKY, S. & BROADUS, J., 1993. On the measurement of biological diversity. *Journal of Environmental Economics and Management*, 24: 60–68.

TEMPLETON, A. R., 1991. Genetics and conservation biology. In: *Species conservation: a population–biological approach*: 15–29 (A. Seitz & V. Loeschcke, Eds.). Birkhauser Verlag, Basel.

THACKWAY, R. & CRESSWELL, I. D., 1995. *An interim biogeographic regionalisation for Australia: a framework for establishing the national system of reserves*. Australian Nature Conservation Agency, Canberra.

VANE–WRIGHT, R. I., HUMPHRIES, C. J. & WILLIAMS, P. H., 1991. What to protect? Systematics and the agony of choice. *Biological Conservation*, 55: 235–254.

WEITZMAN, M. L., 1992. On diversity. *The Quarterly Journal of Economics*, 107: 363-405.

WHITING, A. S., LAWLER, S. H., HORWITZ, P. & CRANDALL, K. A., 2000. Biogeographic regionalization of Australia: assigning conservation priorities based on endemic freshwater crayfish phylogenetics. *Animal Conservation*, 3: 155–163.

WILLIAMS, P. H. & HUMPHRIES, C. J., 1996. Comparing character diversity among biotas. In: *Biodiversity: a biology of numbers and difference*: 54–67 (K. J. Gaston, Ed.). Blackwell, Oxford.

WILLIAMS, P. H., HUMPHRIES, C. J. & GASTON, K. J., 1994. Centers of seed plant diversity: the family way. *Proceedings of the Royal Society, Biological Sciences*, 256: 67–70.