

Biogeographical concordance and efficiency of taxon indicators for establishing conservation priority in a tropical rainforest biota

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Prioritizing areas for conservation requires the use of surrogates for assessing overall patterns of biodiversity. Effective surrogates will reflect general biogeographical patterns and the evolutionary processes that have given rise to these and their efficiency is likely to be influenced by several factors, including the spatial scale of species turnover and the overall congruence of the biogeographical history. We examine patterns of surrogacy for insects, snails, one family of plants and vertebrates from rainforests of northeast Queensland, an area characterized by high endemism and an underlying history of climate-induced vicariance. Nearly all taxa provided some level of prediction of the conservation values for others. However, despite an overall correlation of the patterns of species richness and complementarity, the efficiency of surrogacy was highly asymmetric; snails and insects were strong predictors of conservation priorities for vertebrates, but not vice versa. These results confirm predictions that taxon surrogates can be effective in highly diverse tropical systems where there is a strong history of vicariant biogeography, but also indicate that correlated patterns for species richness and/or complementarity do not guarantee that one taxon will be efficient as a surrogate for another. In our case, the highly diverse and narrowly distributed invertebrates were more efficient as predictors than the less diverse and more broadly distributed vertebrates.

Keywords: biodiversity; complementarity; indicator taxa; reserve selection; tropical rainforest; Australia

1. INTRODUCTION

The setting of conservation priorities among areas within tropical rainforest systems is urgent, but is also generally constrained by the paucity and biases of information on the taxonomy and distributions of species (Nelson *et al.* 1990; Kress *et al.* 1998; Lawton *et al.* 1998). This leaves no choice other than to use as surrogates either environmental variables or indicator taxa; groups of plants or animals whose distribution patterns are assumed to predict those for other biota (Prendergast *et al.* 1999; Margules & Pressey 2000). In practice, several studies have demonstrated poor to moderate correspondence between taxa in their geographical patterns of species richness and/or complementarity (Prendergast *et al.* 1993; Dobson *et al.* 1997; Flather *et al.* 1997; Van Jaarsveld *et al.* 1998; Virolainen *et al.* 2000). These observations have led some to question the value of such assessments for planning at the geographical scales relevant to practical conservation planning (Reid 1998). In order to make further progress on this question, we need to move beyond assessments of patterns and consider the underlying biogeographical and evolutionary processes and, thus, identify situations in which we can reasonably

expect indicator taxa to be efficient predictors of geographical patterns of diversity in others. This, of course is just one contributor to conservation 'value' or 'priority', others include the viability of key species and ecosystem processes.

The efficiency of one taxon as an indicator of conservation priorities for others is likely to depend on the information content relative to the scale of analysis and on whether that taxon has a biogeographical history common to other taxa (Pimm & Lawton 1998). Species-rich taxa with a high proportion of local endemics will have correspondingly high between-area diversity and will be the most informative in assessments based on complementarity (Pressey *et al.* 1993). A common pattern of biogeography depends on either (i) the inclusion of multiple environments, each with a distinct evolutionary history, or (ii) in a more homogeneous system, a spatially congruent history of speciation, extinction and dispersal. The former was responsible for strong correspondence in the geographical patterns of complementarity and, thus, conservation priorities in forest areas of Uganda (Howard *et al.* 1998), whereas the latter has not been explored explicitly in terms of patterns of complementarity and conservation priorities.

In the present study, we examine the effect of biogeographical congruence on conservation assessments across subregions of the rainforests of tropical northeast Queensland. Specifically, we test the efficiency of

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surrogacy for four groups, namely terrestrial snails, selected insects, vertebrates and the plant family Lauraceae, in each case restricting our attention to species that are endemic to the rainforests of the region. All groups show high species diversity and endemism (table 1) and, unusually for a tropical rainforest, their distribution patterns are well documented (see Methods). Among the animals, the species of snails and insects have finer-scale distribution patterns and higher local endemism than those of the vertebrates and plants (table 1). Furthermore, by subdividing the insects into winged versus wingless species, we are able to examine the effect of vagility on local speciation/extinction processes and, thus, on surrogacy. As expected (Darlington 1943), flightless insects had smaller ranges and a higher proportion of local endemics than their winged relatives (table 1). Similarly, on the basis of the biogeography of lineages, we separated snails into taxa that are presumed to represent ancient (Gondwanan) versus recent (post-Miocene) lineages in the wet tropics in order to test the hypothesis that more recently derived species might better reflect historical biogeography within the region.

The rainforests of northeast Queensland are small in area (less than 1 million ha) but are recognized as a World Heritage Area because of their extraordinary biological richness and biogeographical uniqueness (Government of Australia 1986). They are distributed across a series of moderate elevation peaks and plateaus, and adjacent coastal lowlands (figure 1), with the endemic fauna (as represented here) being concentrated in the upland areas. Palaeo-ecological evidence indicates that these rainforests were geographically restricted during the last glacial maximum (Nix 1991; Hopkins *et al.* 1993) and perhaps for much of the Quaternary era (Kershaw 1994) and expanded from mountain tops or other mesic refugia during the early Holocene era. There is little evidence for the endemic vertebrates that these repeated cycles of refugial isolation and expansion have promoted speciation (Schneider *et al.* 1998, 1999; Schneider & Moritz 1999). Rather, it seems that the major effect of the Quaternary climate cycles was local extinction, resulting in qualitatively similar geographical patterns of species richness across rainforest-restricted birds, mammals, frogs and reptiles (Williams & Pearson 1997; Schneider *et al.* 1998).

2. METHODS

Our analysis maximizes the potential for spatial congruence between taxa in two ways: (i) by using previously identified (Williams *et al.* 1996) biogeographical subregions as the spatial unit, and (ii) by analysing only rainforest species that are endemic to the region. The total dataset consists of 627 species and, excluding vertebrates (see below), includes 7283 non-duplicate records (table 1). Geographical records for insects (primarily sucking bugs, particularly Aradidae, and beetles, particularly Carabidae, Tenebrionidae and Scarabaeinae) and terrestrial snails were obtained from extensive sampling across all of the upland areas supplemented by altitudinal transects and opportunistic records (Monteith 1996*b*; J. Stanisic, unpublished data). With increased sampling effort over the past 10 years, the species discovery curve for these groups of insects in the wet tropics has reached a plateau (Monteith 1996*a*). Point records for plant species of the family Lauraceae were obtained from

Table 1. Number of species, records, median number of subregions occupied and per cent of single subregion endemics for the taxonomic groups and subgroups.

(An asterisk indicates that vertebrate distributions are summarized as present within subregions (Williams *et al.* 1996) rather than point records.)

group	number of endemic species	number of records	median number of subregions occupied (total = 23)	single subregion endemics (%)
vertebrates	64	*	11	11
plants	43	1148	4	12
insects	330	4209	2	43
winged insects	71	1477	3	42
wingless insects	259	2732	2	45
snails	190	1926	2	46
Gondwanan	95	566	1	56
post-Miocene	91	1239	2	37

herbaria records. This family was selected because of extensive and verified distributional data, and a stable taxonomy resulting from recent revisions (Hyland 1989; Hyland *et al.* 1999).

The most extensive compilation available for vertebrates (Williams *et al.* 1996) lists species by biogeographical subregion rather than point records. This restricted our analyses to this spatial scale, with areas mostly representing spatially discrete upland areas and adjacent lowlands (figure 1). With regards to management, analysis of areas at this geographical scale can inform regional planning in relation to priorities for rehabilitation, control of visitor access, weed and feral control, and conversion to National Park areas.

Twenty-three biogeographical subregions were used in the analyses (figure 1). Although our emphasis is on the upland areas that are richest in endemic fauna, we have included the adjacent lowland subregions (where invertebrate sampling is less extensive) for comparison. Correlations between taxa for species richness by subregion were tested using Spearman rank correlation. Correlations between taxa for complementarity of species were assessed using Bray–Curtis dissimilarity values for species composition and rescaled to a multivariate distance using semi-strong hybrid multidimensional scaling in Pattern Analysis Package (PATN; Belbin 1991) followed by matrix correlation (Smouse *et al.* 1986).

Subregions were selected for each taxon in order to maximize the rate of species accumulation using an iterative process based on estimated summed irreplaceability, which is defined as the sum of the likelihoods for all species that a subregion would be required as part of a network of sites in order to achieve a set target, in this instance the representation of each species at least once (Pressey *et al.* 1993; Ferrier *et al.* 2000). Irreplaceability is based on the concept of complementarity. However, it also incorporates a measure of the relative importance of an area in achieving an explicit conservation target (Ferrier *et al.* 2000). The efficiency of one taxon as a surrogate for other 'target taxa' was determined using a species accumulation index, that is $SAI = (s-r)/(o-r)$, where s , r and o are the areas under the species accumulation curves using iterative irreplaceability analysis of the surrogate (s), or the target group (o), or random addition of sites (r) (Ferrier & Watson 1997; Ferrier 2001). In

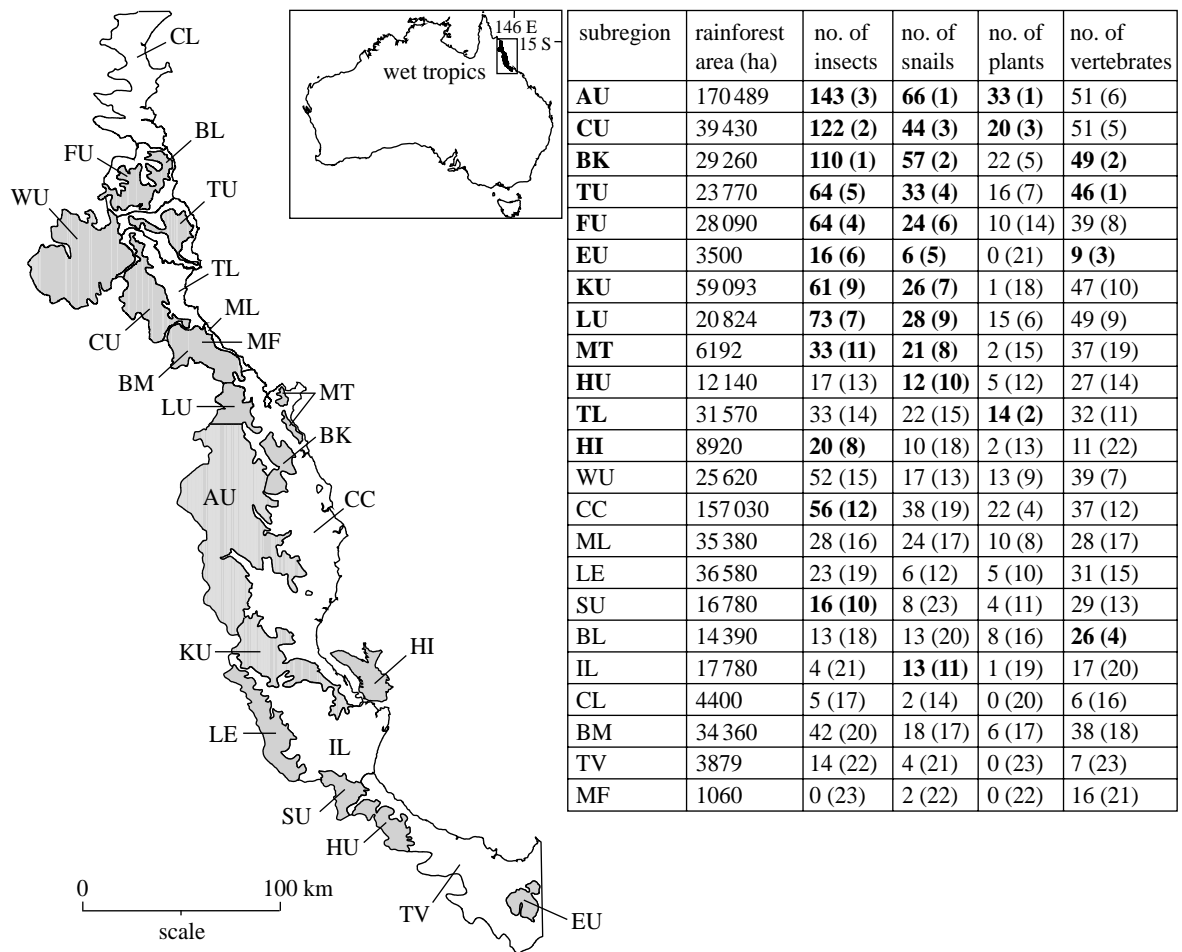


Figure 1. Subregions of the wet tropics rainforest area and number of species for each taxon. Upland regions above 300 m are indicated in grey. The list of subregions from top to bottom reflects the rank order of subregions selected for capturing each species at least once. Parentheses indicate the rank order of the subregion when only the target group is used to select areas. Bold indicates the subregions required to represent 95% of each group. After Williams *et al.* (1996). CL, Cooktown Lowlands; BL, Bloomfield-Helenvale Lowlands; FU, Mount Finnigan Uplands; TL, Thornton Lowlands; TU, Thornton Uplands; WU, Windsor Uplands; ML, Mossman Lowlands; CU, Carbine Uplands; MF, Macalister Foothills; BM, Black Mountain Corridor; CC, Cains-Cardwell Lowlands; LU, Lamb Uplands; MT, Malbon-Thompson Uplands; AU, Atherton Uplands; BK, Bellenden-Ker/Bartle Frere; KU, Kirrama Uplands; HI, Hinchinbrook Island; IL, Ingham Lowlands; LE, Lee Uplands; SU, Spec Uplands; TV, Townsville Lowlands; HU, Halifax Uplands; EU, Elliot Uplands.

contrast to some previous analyses that focus on whether a surrogate performs better than random addition of sites (e.g. Howard *et al.* 1998), this index is scaled to measure the performance of surrogates relative to the difference between optimum (species accumulation using the target taxon itself) and random addition of sites. Statistical tests for differences in the index were based on bootstrap resampling of the subregions (Ferrier & Watson 1997; Ferrier 2001). Two null hypotheses were tested for each pair of surrogate and target taxa: (i) the performance of the surrogate is no better than that achieved by random selection of subregions (i.e. SAI = 0), and (ii) the performance of the surrogate is no worse than that achieved by using the data for the target taxon itself for selecting subregions (i.e. SAI = 1). In this paper, the second null hypothesis is given more attention than the first because it provides a more stringent test of surrogate performance. The significance levels resulting from the individual tests were adjusted in order to account for multiple testing (Rice 1989).

3. RESULTS

(a) *Species richness and complementarity*

The richness of endemic species varied from 293 for subregion AU to just 13 for subregion CL and was correlated with rainforest area ($r=0.64$ and $p < 0.001$) (see figure 1 for subregion abbreviations). In general, richness was highest across all groups in upland subregions, particularly for subregions AU, BK, CU, LU and TU. Two lowland subregions, CC and TL, were also rich in endemic species, in particular plants. The richness values for all 23 subregions were correlated between taxa. The richness values for the 15 upland subregions were also correlated (table 2).

Matrix correlations of complementarity across all subregions and the upland subregions revealed a similar geographical structure for vertebrates, insects, snails and plants (table 2). In particular, multidimensional scaling

Table 2. Matrix of the correlations between taxa across 15 upland subregions for richness (lower) and complementarity (upper).

group	insects	plants	snails	vertebrates
insects	—	$r=0.55$, $p < 0.001$	$r=0.09$, $p=0.082$	$r=0.56$, $p < 0.001$
plants	$r=0.90$, $p < 0.001$	—	$r=0.25$, $p=0.005$	$r=0.28$, $p=0.0016$
snails	$r=0.96$, $p < 0.001$	$r=0.89$, $p < 0.001$	—	$r=0.47$, $p < 0.001$
vertebrates	$r=0.79$, $p < 0.001$	$r=0.68$, $p < 0.001$	$r=0.76$, $p < 0.001$	—

for the faunal groups revealed clear geographical groupings of subregions from north and south of the BM region (data not shown), the site of major vicariance in the system (Nix 1991; Schneider *et al.* 1998). Complementarity scores were significantly correlated between taxa, with the exception of the snail and insect matrices (table 2).

(b) *Efficiency of surrogates*

More than 80% of all species in the 23 subregions in the analysis were represented in just five upland subregions, namely subregions AU, CU, BK, TU and FU (figure 1). These subregions are the highest ranked for both snails and insects, and are prominent for vertebrates and plants, although one lowland subregion (BL) is ranked fourth for vertebrates, and two species-rich lowland sites (TL and CC) are important for plants.

With the exception of vertebrates as surrogates for plants, all indicator taxa performed better than random addition of sites in capturing species diversity for the target group. Tests of the performance of indicator taxa using the SAI revealed a complex but intriguing picture dominated by asymmetrical patterns of effective surrogacy (figure 2). Both insects and snails were highly effective as surrogates for vertebrates relative to optimum addition of sites, and plants were reasonably effective. Snails were reasonably effective as surrogates for plants relative to optimum addition of sites, but insects performed significantly worse, although better than random selection. Insects and snails were adequate as surrogates for each other, but neither plants nor vertebrates were adequate as surrogates for insects or snails. Whereas plants were reasonable predictors for vertebrates, vertebrates did not perform adequately as surrogates for any other group.

The respective separations of insects and snails into winged versus wingless, and recent versus ancient, demonstrated only slight differences in their efficiency as indicators. Flightless insects were weak as surrogates for snails as a target (SAI = 0.85 and 95% confidence interval (CI) = 0.88–0.81) ($p=0.009$), but performed significantly better than winged insects relative to optimum addition of sites (SAI = 0.82 and 95% CI = 0.86–0.76) ($p=0.001$), and both were better than random addition. Similarly, recent snail lineages performed better as surrogates for insects relative to optimum addition of sites (SAI = 0.87 and 95% CI = 0.90–0.83) ($p=0.015$) than did ancient lineages relative to optimum addition of sites (SAI = 0.80 and 95%

CI = 0.85–0.76) ($p < 0.001$), and the latter was no better than random addition ($p=0.20$). The same pattern was observed with plants as the target group relative to optimum addition of sites (recent snails, SAI = 0.91 and 95% CI = 0.94–0.86) ($p=0.018$) and ancient snails, (SAI = 0.87 and 95% CI = 0.93–0.74) ($p < 0.001$), and no different from random addition. The different partitions of snails and insects were equally effective as surrogates for vertebrates.

4. DISCUSSION

In response to the critique of Reid (1998), Balmford (1998) suggested that taxon surrogates for biodiversity may be more effective in tropical than temperate systems because of the greater species richness and spatial heterogeneity of the former. Our analysis of selected taxa that are endemic to the rainforests of northeast Queensland offers evidence that this is true, at least at the scale of biogeographical subregions. With few exceptions (e.g. vertebrates as a surrogate for plants), each indicator taxon proved better than random addition of sites at capturing species diversity for the target taxon. However, using the more stringent criterion that a surrogate should perform as well as the target group itself, the insects and snails clearly outperformed the other groups, acting as strong predictors for vertebrates and reasonably so for plants. However, despite correlations for both richness and complementarity, these predictive relationships were asymmetrical with insects and snails acting as strong surrogates for vertebrates, but vertebrates acting as relatively poor predictors of any of the target groups (figure 2).

Given the widespread use of vertebrates and flowering plants as indicators of biodiversity assessment (Reid 1998), the observed asymmetry is a matter of some concern. We suspect that the stronger performance of insects and snails as surrogates is due to a combination of finer-scale distribution (i.e. local endemism) (table 1) and greater species richness, both of which act to increase information content. This accords with a previous study of biodiversity in the forests of northeast New South Wales, which found that species of ground-dwelling arthropods showed substantial geographical turnover after removing the effects of environmental differences, whereas vertebrates did not (Ferrier *et al.* 1999). The effect of scale on distribution is particularly evident for the AU subregion. This topographically heterogeneous area is the largest subregion analysed, and includes the Atherton Tablelands proper and several adjacent ranges that are considered to be barriers to invertebrate species (Monteith 1996b). Whether taxa with a high degree of spatial heterogeneity (turnover), such as insects and snails, are always better surrogates than more homogeneous taxon, such as vertebrates, may depend on whether a geographical region has historically contained significant dispersal barriers to that taxon, thus creating ecologically equivalent vicariants (Ferrier *et al.* 1999). One way of testing this is to examine surrogate efficiency at different spatial scales. Our present analyses are constrained by the vertebrate data and future studies will vary the spatial scale of analysis.

In the present case, the relatively small number of endemic plant and vertebrate species is clearly a

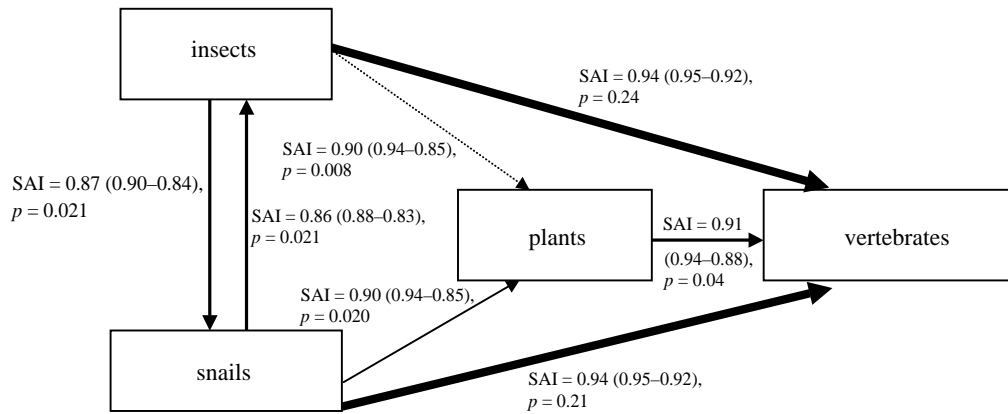


Figure 2. Summary pattern of surrogacy. The thickness of line indicates the difference between the surrogate (s) and the optimum (o) addition of sites and the strength of surrogate efficiency. A thick line indicates no significant difference in performance between the optimum addition of sites and the surrogate ($p > 0.05$); a thin line indicates a weaker, non-significant difference between the optimum addition of sites and the surrogate ($0.05 > p > 0.01$); a broken line indicates a marginally significant difference between the optimum addition of sites and the surrogate ($0.01 > p > 0.001$); and no line indicates a significant difference between the optimum addition of sites and the surrogate ($p < 0.001$). The parentheses after the SAI values indicate the 95% confidence intervals. The SAI values for vertebrates as surrogates for plants, snails and insects as the optimum are respectively: 0.86 (0.92–0.79), $p \leq 0.001$; 0.82 (0.96–0.76), $p < 0.001$; and 0.83 (0.88–0.79), $p < 0.001$. The SAI values for plants as surrogates for snails and insects as the optimum are respectively: 0.81 (0.85–0.74), $p < 0.001$; and 0.82 (0.87–0.76), $p < 0.001$.

constraint; 95% of the species of plants and vertebrates were represented in the top three and four subregions, respectively, whereas 11 subregions were required in order to capture 95% of snails and 12 subregions were required in order to capture 95% of insects. The obvious solution for plants is to add more families to increase the total number and ecological range of species included; the Lauraceae comprise *ca.* 11% of the endemic rainforest tree species of northeast Queensland and 10% of the local endemic tree species (T. Whiffin and B. Hyland, unpublished data). The efficiency of surrogacy for the vertebrates may be improved by including phylogeographical subdivisions within species (Moritz & Faith 1998) and/or using comprehensive point locality data. The former is justified by the presence of morphologically cryptic, but strong and geographically congruent, phylogeographical divisions within widespread vertebrate species from the region (Joseph *et al.* 1995; Schneider *et al.* 1998; Schneider & Moritz 1999).

At the outset we surmised that, because of its underlying history of climate-induced vicariance among upland regions, the wet tropics biota would provide a test for the hypothesis that taxa with a common biogeographical history would be effective as surrogates for each other (Pimm & Lawton 1998). The correlations of richness and complementarity observed between taxa need not indicate reciprocal effectiveness as surrogates and this was demonstrated by the asymmetry of the effectiveness of surrogates using the SAI. Although the results are encouraging, there may still be sufficient differences between taxa in their biogeographical history to warrant caution. Even allowing for sampling bias, it is clear that the diversity of endemic species is consistently higher in upland regions for fauna (Monteith 1996*a,b*; Williams *et al.* 1996), whereas the Lauraceae, in keeping with general observations from

plants (Webb & Tracey 1981), also have peaks of species richness in the very wet lowland subregions (CC and TL) (figure 1). The majority of vertebrate species so far examined predate the Quaternary climate fluctuations (Moritz *et al.* 1997), and analyses of both geographical patterns of endemism (Williams & Pearson 1997) and molecular phylogeography (Schneider *et al.* 1998; Schneider & Moritz 1999) indicate episodes of isolation within refugia and subsequent expansion, most recently in the early Holocene era (e.g. Winter 1997). Although some general patterns are evident (the colonization of subregions HU and SU from the north, and of subregion WU from the east; Schneider *et al.* 1998), the effect of these potentially idiosyncratic events is to overwrite geographical patterns derived from longer-term history. By contrast, it is plausible that taxa with smaller present-day range size and lower vagility, i.e. the snails and insects, may have survived in smaller refugia and, thus, retained more of the underlying biogeographical signal. The presence of endemic insects and snails at subregion HU, and molecular phylogeographical information for one species of snail (*A. Hugall*, unpublished data), support this notion. In this context, it is surprising that there was not a greater difference in the performance of wingless versus winged insects and recent versus ancient snails, although the observed differences were in the directions predicted.

In relation to the prioritization of areas for conservation effort in the wet tropics region, we note that our analysis is based on maximizing the complementarity of endemic species. Although, this is one of many possible conservation objectives, it is probably the most important conservation objective for northeast Queensland, and our results allow for comparison with similar studies in other tropical areas (e.g. Howard *et al.* 1998; Van Jaarsveld *et al.* 1998). Our analysis is also biased towards faunal groups

with a high diversity of endemic species in upland areas. Considering just these subregions, the five highest priority subregions (AU, CU, BK, TU and FU) have previously been suggested as containing refugia for rainforests during the climate fluctuations of the Quaternary era (Webb & Tracey 1981; Nix 1991; Schneider *et al.* 1998), although these refugia were dissected by dry and fire-prone vegetation during the arid extreme of the last glacial maximum (Hopkins *et al.* 1993). By contrast, the lower-ranked upland subregions (HU, SU, LE and WU) are inferred to have been reduced to the extent that endemic vertebrates disappeared and then recolonized during the Holocene era (Williams & Pearson 1997; Winter 1997; Schneider *et al.* 1998). The majority of the rainforests in each of the five high-priority subregions are included within the Wet Tropics World Heritage Area, adding higher levels of protection and increased resources. However, the AU subregion, which is ranked highest for biodiversity value, has been subject to substantial fragmentation of rainforest as a result of clearing for dairy cattle pasture, leading to local extinctions or more subtle impacts on fauna (Laurance 1994; Sumner *et al.* 1999). Perhaps the most significant result is the high priority accorded to subregion EU, a small and isolated area of rainforest to the south of the region. Although relatively depauperate in species endemic to the region, this area contains 17 locally endemic species of fauna, some with phylogenetic affiliations to the wet tropics and others to the rainforest fauna of mid-east Queensland (e.g. Couper *et al.* 2000), as well as geographical isolates of mid-east Queensland species (not included here). By contrast, none of the 16 species of Lauraceae (and, more generally, no rainforest tree species) found in subregion EU are endemic to the wet tropics region. Rather, for plants, subregion EU contains northern isolates of species that are otherwise found in rainforests from mid-east Queensland and further south (T. Whiffin and B. Hyland, unpublished data).

The relatively good efficiency of surrogate taxa, in particular snails and insects, at the scale of the biogeographical subregions of the wet tropics should not be extrapolated to finer spatial scales (Flather *et al.* 1997; Reid 1998). Effective conservation planning within these priority subregions will require reanalysis of the data at the scale of cadastral units using a combination of point records, modelled distributions, environmental layers and consideration of ecological processes in order to ensure persistence (Margules & Pressey 2000). Allowing for this limitation, we support the call (Balmford 1998) for further evaluation and, where appropriate, the use of biodiversity surrogates in species-rich tropical systems where common biogeographical and evolutionary processes are plausible.

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