

EVOLUTION OF SAPROXYLIC AND MYCOPHAGOUS COLEOPTERA IN NEW ZEALAND

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Abstract—Beetles are an old holometabolous group dating back to the early Permian and associated with sediments containing conifers, ginkgos, and cycads. To determine the antiquity of dead wood beetles the evolution of gondwanan saproxylic and mycophagous beetles was examined in the context of available phylogenies that include New Zealand taxa. Phylogenetic position and branch lengths showed that 50 percent of the New Zealand fauna is basal and may represent old lineages dating to around 82 million years when New Zealand separated from Gondwana. Meanwhile, 60 percent of the New Zealand taxa have relatively long branches relative to overseas outgroups and this phenomenon may have resulted from the adaptation of these groups to resource shifts in changing forest communities. The resource shift hypothesis predicts that polyphagy will be widespread in mycophagous and phytophagous insects. Podocarp-broadleaf forest associations are more primitive than associations with *Nothofagus* based on species level phylogenies and forest associations of long-branched taxa.

INTRODUCTION

Though my work as a systematist is geared to develop classifications, build keys, and provide monographs that collate natural history and taxonomic data, most of the contributors and readers of this volume may be chiefly interested in the ecology of dead wood insects. I believe that the time is ripe for ecologists and systematists to build a common research program and it may be useful to introduce some of the readers to what can happen in the field of ecological phylogenetics. Moreover, it may help some ecologists to appreciate that taxonomists are not just folks who are interested in building collections, eager to obtain a few specimens in exchange for a service identification, but are scientists keen to place their knowledge about natural history in a broader scientific context.

The insect order Coleoptera is one of the most important taxa associated with dead wood (Grove 2002). It is the largest group of described organisms and beetles occupy almost every niche available in dead wood (and outside of it). Because of their immense diversity, microhabitat associations and behaviors, beetles are popular subjects for ecological studies. But what about their evolution? How did modern saproxylic communities come into existence? In this essay I report on phylogenetic work in progress and discuss the evolution of saproxylic beetles at deeper evolutionary time scales. First, I briefly review data that indicate that the earliest beetles may have been saproxylic. Then I focus on two phylogenetic questions about saproxylic beetles in New Zealand: (1) are New Zealand taxa basal with respect to other members of their clade, and (2) do they have longer branches compared to their sister taxa located in other areas? Both questions relate to the uniqueness of beetle faunas in the geologically diverse and geographically isolated archipelago of New Zealand.

ANCIENT SAPROXYLIC BEETLES

Beetles are holometabolous insects defined by a suite of adult synapomorphies that include hardened forewings or elytra that enclose the abdomen and flight wings while resting.

These features are thought to be characters that form part of an adaptive complex that led to the extraordinary number of beetle species that exists today. There are four suborders, Archostemata, Adephaga, Polyphaga, and Myxophaga. The first three have many saproxylic species, and the fourth may do so (Löbl 1995). The relationships among the four suborders are controversial (see reviews in Lawrence 1999, Kukulová-Peck and Lawrence 2004, Leschen and Beutel 2004) with many studies supporting Archostemata as sister taxon to the other suborders (compare Beutel and Hass 2000 to Kukulová-Peck and Lawrence 1993, 2004). The Archostemata have a number of primitive characteristics (plesiomorphies), and the common belief that they are a primitive group in Coleoptera is matched by the fossil record. The first true beetles are Archostemata recorded from the early Permian (265 my) and placed in the family Tshekardocoleidae, a short-lived family ranging from the early Permian to early Triassic (Ponomarenko 1969, 2002). But the Archostemata, as defined by Ponomarenko (2002), may be paraphyletic (see Kukulová-Peck and Lawrence 2004) and some of its members, including Tshekardocoleidae, may be placed separately in the order Protocoleoptera.

Part of the phylogenetic debate surrounding the ordinal phylogeny of beetles is the presence of many derived characteristics in Archostemata (Lawrence 1999), a group that has undergone considerable radiation (even though it is rather depauperate at present). The suborder includes rostrate forms from the Triassic (Obrieniidae was described by Zherikhin and Gratshev (1993) as belonging among the weevils (Polyphaga), but were later transferred to Archostemata (Zherikhin 2002)), and unusual life histories, including thelytokous development with viviparous, larviform females in the family Micromalthidae (Pollock and Normark 2002).

Nevertheless, the antiquity of Archostemata is unmatched by any other beetle group, with extant genera dating back to the early Jurassic (*Omma* Newman and *Tetraphalerus* Waterhouse; Zherikhin 2002). At the Permian dawn of Coleoptera,

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conifers were on the rise while the first ginkgos and cycads emerged, and so Ponomorenko (1969) and others (Crowson 1975, Kirejtshuk 2003) speculate that the early Archostemata had xylomycetophagous larvae, based on modern feeding habits. Though there are clear indications of ancient wood boring in fossil wood (Weaver and others 1997) that may have been caused by beetles, trace and fecal fossils are not affirmative (Labandeira 1998), and differentiating between species that feed on decayed or live wood (Zherikhin 2002) is problematic. Meanwhile, the most primitive groups of extant beetles have mouthparts that are associated with feeding on materials such as microfungi and algae (Crowson 1981, Lawrence 1989), and this type of microphagy (Betz and others 2003, Leschen 1993) may have been a primitive feeding mechanism. The presence of microphagous feeding mechanisms suggests that the diets of ancient beetles were not strictly wood feeding and beetles may have occurred in any decaying habitats that promote fungal growth (Personal communication. 2005. John F. Lawrence, Systematist, CSIRO Entomology, GPO Box 1700, Canberra, ACT, 2601, Australia). Because of the rise of conifers with their cork-cambium layer that is easily separated from heartwood after death, it is quite likely that the subcortical situation may have been one of the microhabitats that ancient beetles first inhabited (Crowson 1984, Ponomorenko 2002).

ANCIENT PHYLOGENETIC PATTERNS IN NEW ZEALAND

One way to gain an appreciation of the antiquity of saproxylic beetles is to study their history in New Zealand, an ancient land with an interesting mix of old endemic species and those that have colonized more recently. There are approximately 5000 described New Zealand beetle species (Klimaszewski and Watt 1997), though there may be up to 10,000 species in total, which are placed into 86 families (Leschen and others 2003): 58 of the families have species associated with dead wood. The total numbers of species rival the number for Britain (just over 4000 species), a country of similar area. But New Zealand's location and history are strikingly different from Britain's (and its fauna is too!).

New Zealand is an island archipelago in the southwestern Pacific, chiefly comprised of two main islands that are presently positioned astride the Australian and Pacific plates. Active tectonism has produced a diverse and complex landscape (Suggate and others 1978). Isolation from Gondwana began around 82 million years ago when New Zealand was separated from Australia by the development of the Tasman Basin (Cooper and Millener 1993) and the rifting of the New Zealand landmass to its present eastward location. By the Oligocene period (c. 35 my) most of New Zealand was submerged. Later, plate collision resulted in a mountain building phase which originated in the Miocene and continues to present day. The result is that the South Island is dominated by the north-south trending Southern Alps, which rise to elevations of nearly 4000 m and extend around 500 km. To the east in the rain shadow of the Southern Alps, the landscape consists of lowlands and basins. The southwest end of the South Island contains extensive fjordlands while the northeast of the South Island terminates in sounds. The South Island is separated from the North Island by the narrow Cook Strait which was formed around 0.5 my ago (Lewis and Carter 1994) and

exists only during periods of high sea-levels. During periods of glaciation and low sealevels the islands are linked. The North Island landscape, by contrast, is a result of the offshore subduction that creates north-south trending axial ranges that absorb plate compression, a volcanic arc, with lines of active volcanoes and a backarc region that is being thinned and is subsiding. The elevations of North Island ranges are lower than the Southern Alps. The north terminates in a long peninsula pointing towards New Caledonia, while the broad middle portion is dominated by East and West Capes, making the North Island appearing spindle-shaped.

The geological history of New Zealand, and its contrasting landforms, make it an ideal model system for biogeographic studies, so it is no surprise that the discipline of panbiogeography has its most fervent supporters here (Craw and others 1999, Hull 1988). New Zealand is home to a unique fauna (like the panbiogeographers). Ratite birds have undergone major extinction in New Zealand, and the once diverse group is now reduced to three species of kiwi that are the delight of conservationists, lay people, and scientists. Because of the presence of these ratite birds, and of tuatara, tailed-frogs (*Leiopelmatidae*), and primitive plants like kauri (*Agathis australis* (D. Don) Lindl. (Araucariaceae)) and whisk-ferns, most biologists consider New Zealand a refuge for ancient lineages that evolved prior to the fragmentation of Gondwana. Likewise, many of the beetles may be relictual and should be of interest from an evolutionary and ecological (conservation) perspective.

So, is the dead wood beetle fauna relictual? One way to test this question is to determine the phylogenetic position of New Zealand beetles in reconstructed phylogenies (cladograms) containing taxa from other areas. Relatively basal (primitive) taxa will be located near the root of trees, while derived taxa will be located in higher branches. In figure 1 clade AB is located at the base and is considered primitive relative to, say, taxon E, which is more derived. Also, do New Zealand

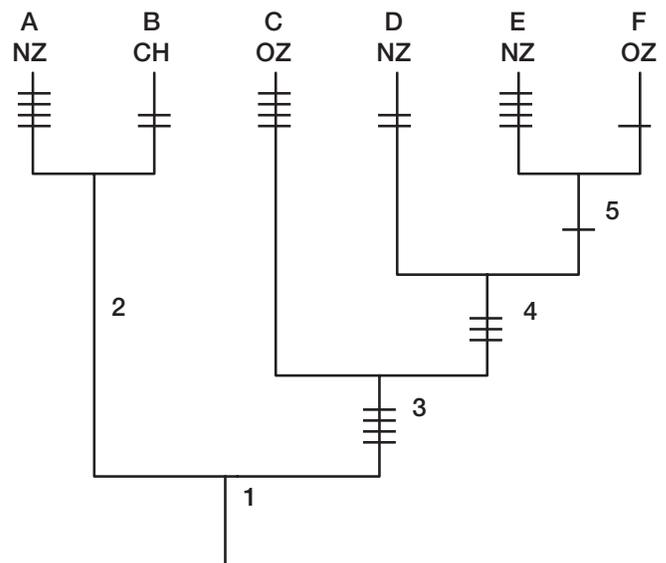


Figure 1—Five-taxon area-cladogram showing distribution of taxa A-F. The bars across each branch indicate character changes (OZ = Australia, CH = Chile, NZ = New Zealand).

taxa have longer branches than their immediate sister taxa? Between the sister pair A and B (fig. 1), A has a longer branch than B. Similarly, taxon C has a longer branch than DEF in this pairwise comparison. The power of the pairwise comparison is the assumption that the time of divergence in a common ancestor calibrates the relative rates of evolution between two sister taxa (Cracraft 1985; Eldredge and Cracraft 1980; Mitter and others 1988; Wiley 1979, 1981). A longer branch will indicate a higher rate of anagenesis compared to that present in a short-branched sister taxon.

METHODS

Addressing questions about phylogenetic location and branch length requires cladograms that include terminal taxa present in and outside of New Zealand; but there are few of these trees available. In fact, monographs and phylogenies are desperately needed to understand the ecology and systematics of all Coleoptera, an issue that limits anyone working on the New Zealand saproxylic fauna. Therefore, I include in the data set any phylogeny that includes saproxylic, leaf litter, and fungus inhabiting beetles (including sooty mould beetles in the endemic families Cyclaxyridae and Agapythidae). These other habitats may be viewed as natural extensions of dead wood since leaf litter will include coarse woody debris of small diameters and fungi of all sorts. A total of 13 phylogenies were used in this study (table 1).

Phylogenetic position in a cladogram is calculated by measuring Relative Phylogenetic Position (RPP) which is the ratio of the node number of the taxon/longest path in cladogram beginning at the root of the tree. An $RPP < 0.50$ is considered relatively basal, while an $RPP \geq 0.50$ is relatively derived. For example, in figure 1 Taxon A is relatively basal with an RPP of 0.25 (1/4) while Taxon E is relatively derived with an RPP of 1.0 (4/4). Branch length is the number of character changes that have occurred since a taxon diverged from its nearest relative. The branch lengths for pairs of two sister taxa with one present in New Zealand and the other occurring elsewhere are compared (these are termed pairwise comparisons by Mitter and others 1988). If the branch length of the New Zealand taxon is longer than its sister taxon, then this is indicative of relatively high rate of evolution compared to its sister taxon.

Measuring these variables, though, is not straightforward. In situations when characters were not mapped onto phylogenies (Lawrence 1994), or onto terminal taxa (Ashe 1992, Hall 1999), branch length was not determined. Where multiple cladograms were published, the one selected as the preferred or reference tree in the original publication was used for this analysis. Polytomies were resolved only when they were located at the base of the tree (Lawrence 1994) or included New Zealand taxa (Pollock 1995). For cases where there is a monophyletic group of New Zealand taxa, branch length and RPP is scored at the basal node (Thayer 1985). If two or more New Zealand taxa are nearest neighbors, then RPP is taken at the basal branch (branch 4, fig. 1) while branch length is measured for the most derived taxon (branch 5, fig. 1), analogous to the situation in biogeography where a sister taxon has become extinct (Paterson and others 1999). This situation occurs in Scaphisomatini (Leschen and Löbl 2005), pilipalpine

Pyrochroidae (Pollock 1995, when the trichotomy is resolved), and Cryptophagidae (Leschen 1996). In the single comparison in pilipalines and the one comparison for cryptosomatulini Cryptophagidae, there are three nearest neighbors (the two taxa used for each of the measurements are listed in table 1).

Nothofagus and podocarp-broadleaf are the two principal forest communities in New Zealand and these forest associations are listed in table 1. Association was based on information contained in original publications and specimens housed in the New Zealand Arthropod Collection, Auckland.

RESULTS

All of 13 phylogenies available for this study were morphology-based (table 1) and included 19 values for RPP and 15 pairwise comparisons for branch length. Ten of 19 (53 percent) taxa were located in basal portions of the trees, and four of these are distributed in podocarp-broadleaf forests, one in *Nothofagus*, and five in both forests. Nine of the 15 (60 percent) pairwise comparisons of branch length had longer branches compared to sister taxa, and three of these taxa are distributed in podocarp-broadleaf forests, one in *Nothofagus*, and five in both forest types. Five taxa are basal and have long branches (*Stylogymnusa*, *Notonewtonia*, *Agapytho*, *Cryptodacne*, and *Loberonotha*), and of these, only *Agapytho* is exclusively found in *Nothofagus*.

DISCUSSION

50 percent of the New Zealand saproxylic taxa were basal and more than half of the taxa had longer branches compared to sister taxa occurring elsewhere. The basal taxa may be relictual and I suggest that they may have had ancestors in New Zealand dating back to 82 my. Whether this pattern is present in other groups of beetles requires the analysis of cladograms for intertidal aleocharine staphylinids (Ahn 2001, Leschen and others 2002), phytophagous weevils (Kuschel and Leschen 2003), and aquatic hydraenids (Beutel and Leschen 2005; Beutel and others 2003) not included in this study.

Determining the phylogenetic position of New Zealand taxa is related to a more comprehensive biogeographic question about the relationships among Earth's biota (Pollock 1995, Sanmartín and Ronquist 2004). A more intensive study of the biogeographic affinities of New Zealand biota will be pursued in a future study that will combine phylogenetic and fossil data for widespread lineages. What is enigmatic, though, is that some old Pangaeian taxa, such as Archostemata, are absent from New Zealand, which suggests that either they were absent here at the time of the fragmentation of Gondwana, or have gone extinct afterwards. One massive extinction event may have occurred in New Zealand during the Oligocene (c. 30 my) marine transgression where there is evidence of a considerable reduction in the land area. Cooper and Cooper (1995) considered this submergence a crisis that created bottle-necks in populations that led to widespread extinctions — some even believe that the entire country was completely submerged (Macphail 1997, Pole 1994). But the presence of ancient beetle lineages in New Zealand provides strong evidence against the hypothesis of total submergence.

Table 1—Taxa examined for position and branch length with their forest associations. For each study referenced, the number of terminal taxa and taxonomic level, and number of characters used are provided

Taxon	RPP	BL	Forest type	Reference
Ptiliidae				
<i>Nellosana</i> Johnson (3 spp.)	0.25	—	P	Hall 1999 (28 genera/48)
Leiodidae				
<i>Catopsilius</i> Sharp (2 spp.)	0.6	Same	P	Leschen and Newton unpubl. (Neopelatopini, 10 genera/25)
n. gen. (7+ spp.)	1.0	Lower	B	“ ”
Staphylinidae				
<i>Metacoraeolabium</i> Steel (7 spp.)	0.1	Lower	B	Thayer 1985 (Omaliinae, 22 spp./34)
<i>Stylogymnusa</i> Hammond (1 sp.)	0.1	Higher	P	Ahn and Ashe 2004 (Aleocharinae, 57 spp./99)
<i>Austrasilida</i> Ashe (1 sp.)	0.6	—	B	Ashe 1992 (Aleocharinae, 26 spp/34)
<i>Brachynopus</i> Broun (2 spp.)	0.3	Lower	B	Leschen and Löbl 2005 (Scaphisomatini, 45 gen/110)
“B.” <i>apicellum</i> (Broun)	—	Higher	P	
“B.” <i>rufa</i> Broun	0.4	—	P	“ ”
<i>Notonewtonia</i> Leschen and Löbl (2 spp.)	0.4	Higher	B ^a	“ ”
<i>Euderia</i> Broun (1 spp.)	0.5	—	N	Philips (2000) (Anobiidae, 34 genera/102)
Erotylidae				
<i>Cryptodacne</i> Sharp (7 spp.)	0.2	Higher	B ^b	Wegrzynowicz 2002 (Erotylinae, 30 gen./85)
<i>Loberonotha</i> Sen Gupta and Crowson (1 sp.)	0.2	Higher	B	Leschen 2003 (Erotylidae, 57 gene/120)
Cryptophagidae				
<i>Ostreacryptus</i> Leschen (1 sp.) ^c	0.4	—	P	Leschen 1996 (55 genera/113)
<i>Picrotus</i> Sharp (2 spp.)	—	Same	B ^d	Leschen 1996 (55 genera/113)
<i>Paratomaria</i> Leschen (1 sp.)	0.6	—	P	Leschen 1996 (55 genera/113)
<i>Salltius</i> Broun (1 sp.)	—	Higher	P	Leschen 1996 (55 genera/113)
Agapythidae				
<i>Agapytho</i> Broun (1 sp.)	0.4	Higher	N	Leschen and others 2005 (36 genera/99)
Priasilphidae				
<i>Priasilpha</i> Broun (7 spp.)	0.5	Lower	B ^b	Leschen and others 2005 (36 genera/99)
Cyclaxyridae				
<i>Cyclaxyra</i> Broun (3 spp.)	0.9	Higher	B ^d	Leschen and others 2005 (36 genera/99)
Ulodidae				
<i>Brouniphylax</i> Strand + <i>Syrphetodes</i> Pascoe (15+ spp)	0.8	—	B	Lawrence 1994 (Zopheridae groups, 20 genera/31)
Pyrochroidae				
<i>Exocalopus</i> Broun (1 sp.)	—	Higher	B	Pollock 1995 (Pilipalpinae, 15 genera/30)
<i>Techmessa</i> Bates (2 spp.)	0.7	—	B	Pollock 1995 (Pilipalpinae, 15 genera/30)

RPP = Relative Phylogenetic Position; BL = branch length; B = both forest types, N = *Nothofagus*, P = podocarp-broadleaf.

^a Most species or specimens present in podocarp-broadleaf forests.

^b Primitive species in these groups are associated with podocarp-broadleaf forests (Skelley and Leschen, submitted in 2005; Leschen and Michaux, in press).

^c Listed as New Zealand genus 2 and named later (Leschen 2001).

^d Most species or specimens present in *Nothofagus* forests.

Meanwhile, the pattern in beetles is testimony to a complex geological and climatic history that influenced the biota of New Zealand since the break-up of Gondwana. Over half of the New Zealand taxa have longer branches than those of their sister taxa. Rate of anagenesis, or the accumulation of character changes within a single branch, has many causes. Assuming no extinction and a constant rate of speciation with random change, I suggest that the high number of long branches present in New Zealand taxa may be indicative of lineages that persisted over time during changing vegetative landscapes, and that these groups had to adapt to periodic introductions (and losses) of new fungal and dead wood resources.

The vegetative history of New Zealand is a story of ever-changing communities associated with loss and gains of many taxa throughout the fossil record (Lee and others 2001). Losses mark each epoch, but none as great as the losses occurring during the Miocene with the extinction of 23 genera. It is also remarkable that the extinction of *Acacia*, *Eucalyptus* and other genera in New Zealand occurred as recently as the Pleistocene. Coupled with the Oligocene bottleneck, these community changes over time must have significantly influenced the evolution of saproxylic beetles. Therefore, long branches may have arisen in lineages as an adaptive response to plant community changes that facilitated resource shifts, especially in saproxylic and fungus beetles that would have had to track dramatic changes in the composition of coarse woody debris. Evidence for resource shifting is that 13 taxa listed in table 1 are associated with both *Nothofagus* and podocarp-broadleaf forests. This hypothesis predicts that saproxylic beetles may be associated with different types of coarse woody debris, and likewise, polyphagy should dominate in phytophagous and mycophagous insects as a result of resource shifting.

One line of evidence against the “resource shift hypothesis” is that beetle and plant communities may be stable in ecological time and have maintained cohesion since the last glacial maximum. Based on new data from the fossil record, communities respond to climate change and are influenced by changes in temperature (Marra 2003a, 2003b; Marra and Leschen 2004) resulting in local extinctions while species continue to survive (Marra, Maureen. [Name of manuscript unknown]. Manuscript in preparation. Author can be reached at: Landcare Research, Private Bag 3127, Hamilton, New Zealand.) (Marra, Maureen; Leschen, Richard A.B. [Manuscript in preparation]. Fossil beetles as indicators of climate change and geological history of New Zealand. Maureen Marra can be reached at: Landcare Research, Private Bag 3127, Hamilton, New Zealand). However, fossil sites are limited to a few Quaternary locations and older sites need to be examined to reconstruct older fossil communities.

The assumptions for the resource shift hypothesis may be too simplistic. For example, one cause for long-branches is the extinction of sister taxa, and this too may result in asymmetrical (unbalanced) trees (Guyer and Slowinski 1993, Heard and Mooers 2002). It would be important to examine the symmetry of phylogenetic trees of saproxylic beetles to determine if tree shape may relate to extinction events such as the Oligocene drowning rather than to resource tracking.

There is also reason to doubt that long branches and basal positions are coupled (see table 1). For example, the New

Zealand kauri is the most primitive member of *Agathis*, a genus that has fossils in New Zealand dating back to the Cretaceous, and has a relatively short branch based on *rbcl* sequences (Stöckler and others 2002). The biogeographic story for plants, however, is much different from that of animals (Sanmartín and Ronquist 2004), with a greater proportion of dispersal than vicariance. It is also expected that the history of different lineages of beetles may differ, which is reflected in the asymmetry between number of basal taxa and those having higher branch lengths. Additional data from molecular clocks and fossils to determine evolutionary rates alongside natural history studies would provide tests of the resource shift hypothesis by providing divergence dates and ages for extant saproxylic taxa.

Determining ancestral community associations for New Zealand saproxylic beetles is hampered by the lack of species level phylogenies and detailed information on their geographic distributions. Thayer (1985) published the only species level phylogeny for New Zealand saproxylic beetles (*Metacorneolabium*, Staphylinidae). Otherwise, there are unpublished cladograms for species of New Zealand *Baeocera* (scaphisomatine Staphylinidae) (Leschen, Richard A.B. Unpublished, phylogeny. Leschen, author of this paper), and the endemic genera *Cryptodacne* (Erotylidae) (Skelley and Leschen 2006, submitted) and *Priasilpha* (Priasilphidae) (Leschen and Michaux 2005). When forest associations are optimized onto these cladograms, podocarp-broadleaf associations are primitive for *Baeocera*, *Cryptodacne*, and *Priasilpha*, while *Nothofagus* may be primitive for *Metacorneolabium*.

In basal and long-branched taxa that are found in both podocarp-broadleaf and *Nothofagus* forests, most of the species and/or specimens are found in association with podocarp-broadleaf forests (table 1). These data mirrors the patterns seen in the species phylogenies that podocarp-broadleaf forest associations may be more primitive than the *Nothofagus* associations. This pattern seems reasonable because of the more recent arrival of *Nothofagus* (Hill 2001, Macphail and others 1994) compared to that of podocarps in New Zealand. Even though Mill (2003) believes that the recent New Zealand podocarps represent a secondary radiation, these forests could have been continuously present since the Cretaceous. It is also possible that more derived species occur in areas dominated by *Nothofagus*, only because many of these areas were recently glaciated (Porter 1975, Trewick and Wallis 2001) and not because of a strict association with forest type.

Classifying forest types into two forest types may be problematic, particularly because the podocarp-broadleaf class includes within it the *Metrosideros* forests of Auckland Island in the New Zealand subantarctic (Campbell Plateau). Optional character state treatments could illuminate different patterns of character evolution (Leschen 1999) and when the podocarp-broadleaf class is separated into two divisions (*Metrosideros* versus podocarp-broadleaf) this creates a more complex character-state reconstruction in *Priasilpha*. The ancestral states in *Priasilpha* are made ambiguous by having a mixture of podocarp-broadleaf, *Metrosideros*, and *Nothofagus* forest associations (Leschen and Michaux 2005). One of the most primitive *Priasilpha* species occurs in the subantarctic *Metrosideros* forests, where it is sympatric with the basal species *Stylogymnusa antarctica* Hammond (table 1). In

contrast to *Nothofagus*, which is recorded from New Zealand in the late Cretaceous (Lee and others 200), fossil pollen (late Paleocene; Mildenhall, 1980) and macrofossils (early Miocene, Pole 1991) of *Metrosideros* are more recent, and members of this genus tend to be climbers in New Zealand. So, it is likely that the basal position of Auckland Island taxa are related more to the age of the Campbell Plateau landmass (Michaux and Leschen 2005) than to the forest type.

The preliminary analysis here is work in progress and indeed there are several biases and problems with it. The small number of available phylogenies, all of which are morphology-based, which by their nature are composed of fewer character changes compared to molecular data, may bias the results. In fact if other groups were included in this study to broaden the questions to include all lineages of terrestrial biota, the results might well change. Also different taxonomic levels were compared across taxa (usually genus-level) and it would be valuable to use trees based on species (but this is a problem when dealing with insect diversity!). On-going work on species- and population-level phylogenies for various mycophagous beetles (e.g., Leiodidae, scaphidiine staphylinids, Nitidulidae) will help to determine ancestral forest associations. These data coupled with species level phylogenies of plant feeding taxa, such as Molytini weevils (Craw 1999), will help to reconstruct community level patterns through evolutionary and ecological time. A test that examines probability of position, character changes, and branch length in a theoretical tree space will also provide the statistical rigor needed to test the patterns illustrated here.

PROSPECTUS FOR ECOLOGICAL AND PHYLOGENETIC STUDIES ON SAPROXYLIC INSECTS

Many ecosystems in New Zealand and elsewhere are under threat, and there are species that have become extinct, or will do so very soon. In New Zealand the fauna has been reduced by human impact (Worthy and Holdaway 2002), including the accidental introductions of rodents (Holdaway 1996) and other predators that are capable of wiping out the larger species of invertebrates that are not lucky enough to have defensive secretions or find refuge on predator-free islands (e.g., Leschen and Rhode 2002). Then there is the accidental introduction of ants (Harris and Berry 2001) that will affect even the smallest arthropod taxa. So there is a need for scientists from all disciplines to combine their skills to address biological questions at all levels before species losses are further accentuated by climate change.

Much has been gained by the incorporation of phylogenetic data into ecological programs (Brooks and McLennan 1993, Gorman 1993) and there has been a recent upsurge in research on populations and species using molecules, even resulting in specialized publications such as the journal *Molecular Ecology*. While some of the papers in *Molecular Ecology* may be organismal, much of the autecological work does little for community ecology and the understanding of natural history for many groups, especially those taxa like dead wood insects that are not easily (and repeatedly) sampled for DNA studies. *Phylogenetic assembly* is a relatively new and promising field that incorporates knowledge of the community in question and the phylogenetic relationships of the co-exist-

ing organisms (see Webb and others 2002 for application and methods). Among several questions that can be addressed about communities, two questions, as covered by Webb and others (2002), are paramount: Is the distribution of species among habitats in a community nonrandom with respect to phylogeny and how are niche differences in communities arrayed on a phylogeny? Several lines of data are needed: a list of species for the local community, their geographic distributions, ecological character data, and phylogenetic data for each of the species. Obviously, a list of insects would be easier to obtain than phylogenies for each species, and in hyperdiverse areas such as tropical rainforests, even a list may be difficult without a team of collaborators. Nevertheless, the protocols of this research program to determine the origin and structure of saproxylic insect communities has the potential to elicit input from biologists of different disciplines and one can imagine the direct applications to insect conservation and management.

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