



# Revealing the factors that promote speciation

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What biological attributes of organisms promote speciation, and ultimately, species diversity? This question has a long history of interest, with proposed diversity promoters including attributes such as sexual selection, ecological specialism and dispersability. However, such ideas are difficult to test because the time-scale of processes involved is too great for direct human observation and experimentation. An increasingly powerful solution is to investigate diversity patterns among extant groups to infer the nature of processes operating during the evolution of those groups. This approach relies on the use of robust, phylogenetically based null models to overcome some of the problems inherent in observational inference. We illustrate this area by (i) discussing recent advances in identifying correlates of diversity among higher taxa, and (ii) proposing new methods for analysing patterns in species-level phylogenies, drawing examples from a wide range of organisms.

**Keywords:** species diversity; species-richness; evolution; diversification; phylogeny; sister group

## 1. INTRODUCTION

Life is made up of species, and so understanding the evolution of species-richness is fundamental to our understanding of the natural world. Traditionally, however, this area is plagued by the difficulties inherent in studying a phenomenon operating over time-scales many orders of magnitude greater than our own lifespans (Panchen 1992). Recent accumulation of phylogenetic information through the use of molecular techniques has provided novel possibilities for statistical tests of hypotheses concerning the evolution of species-richness in extant taxa (Moore & Heard 1997; Nee *et al.* 1996a; Purvis 1996; Sanderson & Donoghue 1996). We illustrate this approach by concentrating on two issues. First, can biological attributes of lineages influence the tendency for those lineages to accumulate species-richness? Second, can we use species-level phylogenies to identify modes of speciation and patterns of subsequent phenotypic change?

## 2. BIOLOGICAL FACTORS PROMOTING SPECIES-RICHNESS

Lineages vary in the number of species they contain. Possible causes for this variation include differences in the environment experienced by those lineages (Cracraft 1985; Ricklefs & Schluter 1993; Rosenzweig 1995; Kerr & Packer 1997), or mere chance variation in probabilities of speciation and extinction (Raup *et al.* 1973; Raup 1985). An additional possibility is that lineages may vary with respect to biological attributes that influence the net rate of cladogenesis, either through an effect on speciation rate or extinction rate, or the equilibrium number of species a lineage can realize. For example, many authors have suggested that strong sexual selection by female choice may promote speciation and ultimately species-richness

(Darwin 1871; West-Eberhard 1983). Similarly, species range size has been postulated as an attribute with a strong effect on extinction probability (Jackson 1974; Jablonski 1987), and small body size has been proposed as an attribute permitting high equilibrium species numbers within lineages (Hutchinson & MacArthur 1959; Morse *et al.* 1985).

To test ideas of this kind we need to look for replicate evidence for an association between the trait of interest and species-richness. A recent approach is to compare sister groups that differ in their expression of the trait in question. There are four reasons why sister-group comparison is currently the best approach for identifying evolutionary correlates of species-richness (Mitter *et al.* 1988; Zeh *et al.* 1989; Barraclough *et al.* 1998).

1. Replication. By including several sister-group comparisons in our tests we gain replicated statistical evidence for any trend we observe. This replication increases our ability to make general conclusions about an effect, reducing the possibility of detecting accidental, historical associations between traits and species-richness (Cracraft 1990).
2. Rates of diversification. Our interest is in testing whether lineages with a particular attribute accumulate more species than those without it. However, different taxa have different ages, and so we might expect older taxa to have more species than younger taxa if they are growing simply because they have had time to accumulate more species. Sister taxa are, by definition, the same age, and so by comparing the number of species between sister groups we obtain direct estimates of relative net rates.
3. Non-independence of taxa. Several taxa may share a high species accumulation rate and the same value of a biological attribute simply because they inherited both

from a common ancestor. In this case these taxa do not represent independent data points supporting an evolutionary correlation between species diversity and the biological variable as both traits have evolved only once. Sister-group comparisons overcome this problem because differences between sister taxa have evolved subsequent to their divergence and so necessarily represent independent evolutionary events (Møller & Birkhead 1992).

4. Confounding variables and noise. Taxa differ in many attributes apart from the trait of primary interest, X, and diversification rate. Some of these attributes may influence diversification rate, causing error variation or noise in the data that may obscure any pattern arising from an effect of trait X on diversification rates. In addition, trait X may have no direct influence on diversification rates, but we may observe a correlation through the influence of unaccounted-for confounding variables. The shared common ancestry of sister taxa means they will tend to be similar to each other in many respects. By comparing sister taxa we are comparing like with like, thereby controlling for much potential noise and confounding variation which might otherwise afflict our analysis (Read & Nee 1995; Harvey *et al.* 1995; Nee *et al.* 1996b).

Two additional features of sister-group comparison should be mentioned with respect to drawing conclusions. First, these tests detect a correlation and so ultimately it is not possible to determine the direction of causation between species-richness and the study variable, nor to rule out entirely the possibility of confounding variables. Second, the approach compares the net rate of cladogenesis between sister taxa and so cannot determine whether effects on speciation or extinction are the cause of any observed patterns. Nonetheless, sister-group analysis has provided new evidence for the role of several biological traits in promoting species-richness. Three examples are provided.

#### (a) *Plant-feeding (phytophagy) in insects*

The first use of sister-group analysis was by Mitter *et al.* (1988) in their test of the widely suggested hypothesis that plant-feeding (phytophagous) insects have enhanced species-richness (Erhlich & Raven 1964; Southwood 1973). They identified all monophyletic groups of exclusively phytophagous insects with a putative non-phytophagous sister taxon, and compared the numbers of species between sister taxa. Under the null model of no association we predict the phytophagous taxon should contain more species than its non-phytophagous sister taxon in roughly half the comparisons. In fact, 11 out of 13 comparisons display greater species-richness in the phytophagous taxon, which is significant under a sign test ( $p=0.011$ , one-tailed sign test). This result is consistent with the view that plant-feeding is a factor that promotes high diversity in insect groups, perhaps through the increased capacity for trophic niche specialization entailed by this lifestyle. This work was followed by similar analyses on the effects of resin canals in plants (positive relationship; Farrell *et al.* 1991), and carnivorous parasitism in insects (no relationship; Wiegmann *et al.* 1993). A general summary of these results is found in Farrell & Mitter (1993).

#### (b) *Sexual selection by female choice in birds*

The second example is the use of sister-group analysis to perform a statistical test of the age-old hypothesis that sexual selection by female choice can increase the rate of origin of reproductive isolation and thereby increase speciation rates and ultimately species-richness (Darwin 1871; Fisher 1958; Lande 1981). Barraclough *et al.* (1995) tested the hypothesis in passerine birds, using sexual dichromatism as an index of the strength of intersexual selection, and the DNA–DNA hybridization phylogeny of Sibley & Ahlquist (1990) to identify sister taxa. They found a significant relationship between the proportion of sexually dichromatic species within clades and the species-richness of those clades, with around 75% of nodes following the pattern expected under the Darwin hypothesis. The result is robust to likely errors in the phylogeny and so is consistent with the Darwin hypothesis. A full discussion of the assumptions underlying this test is presented elsewhere (Barraclough *et al.* 1995). Subsequent work has confirmed a similar pattern with an alternative measure in birds (mating system; Mitra *et al.* 1996), and found evidence for a related effect in flowering plants (nectar spur length; Hodges & Arnold 1995).

#### (c) *Rate of molecular evolution in birds and plants*

The final example is the use of sister-group comparisons to investigate the relationship between the rate of species accumulation and rates of genetic change in flowering plants (Barraclough *et al.* 1996). Chase *et al.* (1993) present a phylogeny of the majority of plant families based on sequence data for the chloroplast gene *rbcL*. Their phylogeny includes information on the number of nucleotide substitutions occurring on branches, and so we can compare branch lengths between sister taxa to compare relative rates of nucleotide substitution (Bromham *et al.* 1996; Mindell & Thacker 1996). Sister-taxon comparisons reveal a significant, positive relationship between branch length (i.e. rate of nucleotide substitution) and the number of species in each family, which is apparently robust with respect to likely errors in the phylogeny and possible artefacts arising from parsimony reconstruction (see Sanderson (1990) for details). A similar, positive relationship is found in passerine birds using DNA–DNA hybridization data from Sibley & Ahlquist (1990; T. G. Barraclough, unpublished results). The finding of a similar relationship for different molecular measures in very different organisms points intriguingly towards a potentially general association between rates of cladogenesis and rates of genetic change. If indeed general, this pattern may reflect the effect of circumstances associated with, or necessary for, speciation on the rate of genetic change (such as population structure; Mayr 1954; Coyne 1992; Templeton 1996; Slatkin 1996); an influence of rates of genetic change on the probability of speciation (Orr 1995; Orr & Orr 1996); or a reduction of extinction risk in lineages with high rates of genetic change. Further publication of large phylogenies will allow systematic tests for a general effect and may allow tests of possible mechanisms underlying these patterns.

In conclusion, sister-group analysis is a simple, but powerful tool for testing hypotheses concerning biological factors that promote species-richness, providing the first statistical evidence for several long standing hypotheses

Table 1. *Sister-group analyses of correlates of species-richness*

Authors	subject area	result
<i>(a)</i> Insects and insect-plant relations		
Mitter <i>et al.</i> (1988)	phytophagy in insects	positive
Zeh <i>et al.</i> (1989)	novel oviposition sites	positive
Farrell <i>et al.</i> (1991)	resin/latex canals in plants	positive
Wiegmann <i>et al.</i> (1993)	parasitic carnivory in insects	none
Connor & Taverner (1997)	leaf-mining in insects	negative
<i>(b)</i> Sexual selection, breeding systems		
Barraclough <i>et al.</i> (1995)	sexual dichromatism in passerines	positive
Hodges & Arnold (1995)	nectar spurs in plants	positive
Mitra <i>et al.</i> (1996)	promiscuity in birds	positive
Mooers & Møller (1996)	colonial breeding in birds	none
<i>(c)</i> Miscellaneous		
Barraclough <i>et al.</i> (1996)	rate of molecular evolution in plants	positive
Gittleman & Purvis (1998)	body size in carnivores/primates	negative/none
McCall <i>et al.</i> (1998)	dispersal ability and island endemism	trade-off

(see list in table 1). Identification of sister groups relies on the availability of large-scale phylogenies, and so inevitably this approach will increase in utility as more phylogenies are published.

### 3. IDENTIFYING MODES OF SPECIATION AND SUBSEQUENT PHENOTYPIC CHANGE

The previous section dealt with identifying biological factors associated with the number of species within lineages of organisms. At a finer scale, phylogenies at the species level provide an estimate of the pattern of splits leading to present-day species, and so may potentially provide information into processes operating during the radiation of a group (Harvey *et al.* 1994; Nee *et al.* 1994). In this section we describe some ways we might extract that information.

In general terms, we can recognize four dynamic events leading to present-day patterns of species-richness. First, new species are formed by speciation, usually through splitting of an ancestral species into two, or potentially more, daughter species (for exceptions, see Grant 1981; Bullini 1994). Second, the geographic ranges of species may change, either by contraction/expansion or by range movements. Third, there are changes in the genotype and phenotype of species. Fourth, there is extinction. Our ultimate goal then is to understand factors influencing each event and any interactions among them. In combination with geographic and ecological data, species-level phylogenies may provide a trace of this process. However, two features must be kept in mind if we are to use this information. First, ranges and phenotypes change over time, as species are buffeted by changing circumstances, and so information of conditions at past events may not be accurately preserved among present-day species. Second, there are a large number of possible interactions between the events outlined above and so it may not always be possible to discriminate precisely between all possible scenarios.

Here, we outline ways in which species-level phylogenies may be used by focusing on two issues: the relationship between geography and species splitting (modes of speciation); and the interaction between

geography and phenotypic evolution, using two lineages of tiger beetles (family: Cicindelidae) from North America as examples.

#### *(a) The role of geography in species splits*

Traditionally, the most important factor causing the splitting of a single species into two is believed to be geography, through the environmental origin of a barrier to gene flow, gradual divergence of geographically structured populations, or establishment of isolated populations through the colonization of a new areas (Mayr 1963; Allmon 1992). The empirical basis for this viewpoint is the observation that closely related sister species tend to be geographically separated with either discontinuous (allopatric) or adjacent (parapatric) geographic ranges (Lynch 1989; Chesser & Zink 1994).

With species-level phylogenies we can look at the pattern of geographic ranges with reference to the entire phylogeny (Lynch 1989). Our approach is to plot the degree of sympatry at each node in the phylogeny against the 'height' of that node, where degree of sympatry is calculated as the mean of the proportion of each clade's area overlapped by the other, and the area of a clade is the range occupied by any of its member species. Note that sympatry in this context refers to the large-scale overlap of species ranges, rather than implying necessary co-occurrence at the finescale. Node height is simply the relative distance of a node from the tips of the phylogeny. This plot can provide some insight into the geographic pattern of speciation.

Under a null model that the geographic ranges of species are random with respect to phylogeny, we expect an increase in sympatry with node height, as shown in figure 1. The increase is expected, as the range of sister clades becomes larger at higher levels simply because the clades include more species, and so the chance of overlap between them is greater, given a finite area. This scenario corresponds to the situation in which ranges have changed so much since species splits that they no longer contain information about ranges at the time of splits.

Different qualitative patterns are expected under alternative geographic models of speciation, shown in figure 2.

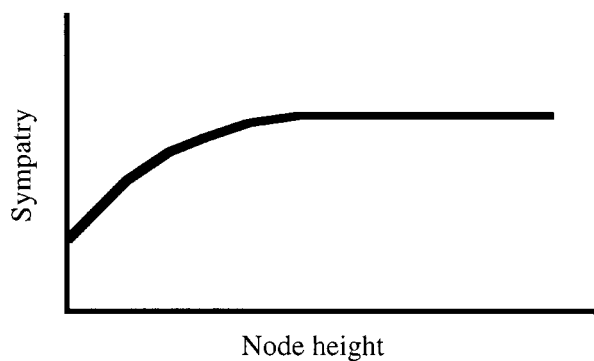


Figure 1. Expected relationship between degree of sympatry and node height under null model that geographic ranges are random with respect to phylogeny.

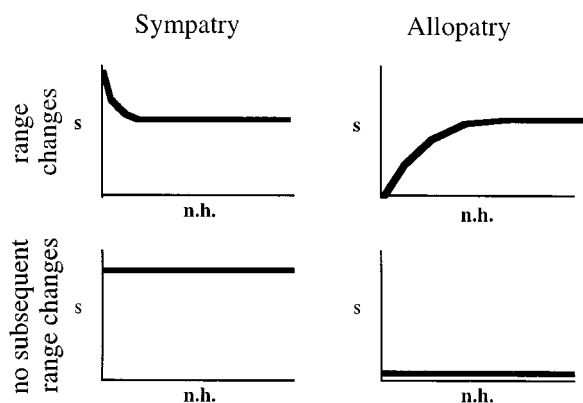


Figure 2. Expected patterns between degree of sympatry ( $s$ ) and node height (n.h.) under alternative geographical models of speciation.

The expectations depend on the geographic mode of speciation and whether range changes have occurred subsequent to speciation. The geographic mode of speciation sets a limit for the expected intercept. If speciation is allopatric we expect an intercept of zero, because very recently split species are expected to display no overlap in ranges. If speciation is sympatric we expect an intercept greater than 0.5, because one of the species must be entirely contained within the other's geographic range immediately following the split. The subsequent pattern of sympatry with node height depends on whether ranges change over time, either through expansion/contraction or drift. If ranges do not change, then there will be no change in sympatry with node height. Otherwise, sympatry will tend to a rough level at which further range expansions/drifts do not tend to increase or decrease the degree of sympatry. In the case of allopatric speciation this necessarily entails an increase in sympatry with node height. This is based simply on the idea that ranges are separated initially due to the allopatric nature of speciation, but are then 'mixed' over time by random influences. In the case of sympatric speciation there may be a slight increase, decrease or no change depending on the exact relationship between the expected intercept and the expected rough equilibrium level of sympatry between older sister clades.

Note that the scenario for allopatric speciation and subsequent range changes is qualitatively similar to the

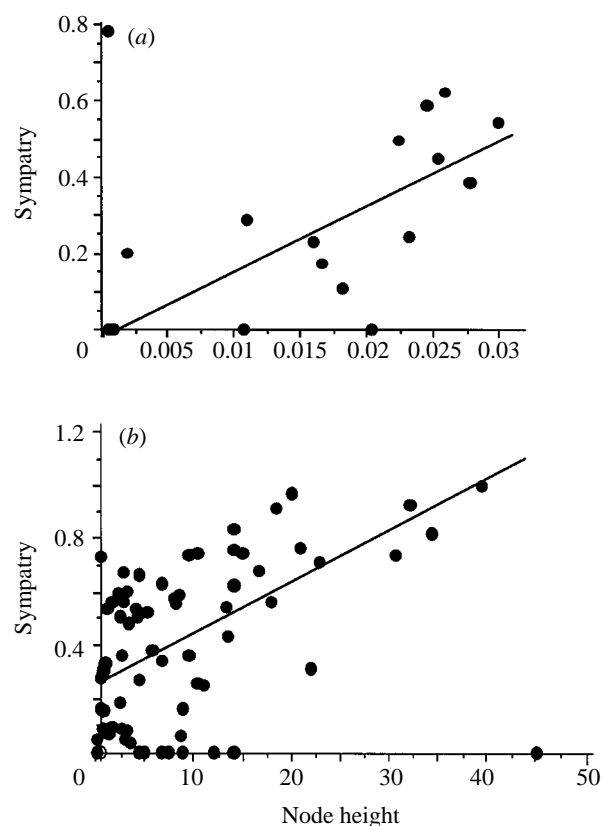


Figure 3. Two examples of plots between sympatry and node height. (a) Phylogeny taken from Smith & Bush (1997), range data from Foote *et al.* (1993). The overall trend is for increasing sympatry with node height, consistent with a model of allopatric speciation, with subsequent range changes. However, recent node with unusually high sympatry represents outlier suggestive of a sympatric speciation event (regression line drawn excluding this point). Note that the genus *Rhagoletis* (North American fruit flies) provides classic examples of sympatric speciation by host shifts (Bush 1969), and yet overall trend appears to be allopatric. (b) Phylogeny of world primates from Purvis (1995), range data from A. Purvis (unpublished data). Only nodes with quoted date estimates in Purvis (1995) are included. Although noisy, the general trend is for increasing sympatry with node height, again consistent with allopatric speciation and range changes. However, the oldest dated split, between Madagascar lemurs and African bush-babies/lorises, is characterized by zero sympatry, and so is an outlier suggestive of an ancient vicariance event.

null expectation of random geographic ranges. However, we expect a zero intercept in the former case, whereas under the null model we are likely to observe some recent splits with considerable geographic overlap simply by chance. Hence, these scenarios may be distinguishable in some circumstances. Note also that the expectations are based on the assumption of uniform process for all nodes, which of course need not be the case. If there is one sympatric speciation event in a group for which allopatric speciation is the norm, this may show up as an outlier with unusually large sympatry for its node height. Similarly, ancient vicariations may show up as nodes with unusually low sympatry for their height. Examples of each case are shown in figure 3.

Can we use this approach to distinguish broad geographical patterns of speciation? We present the example of

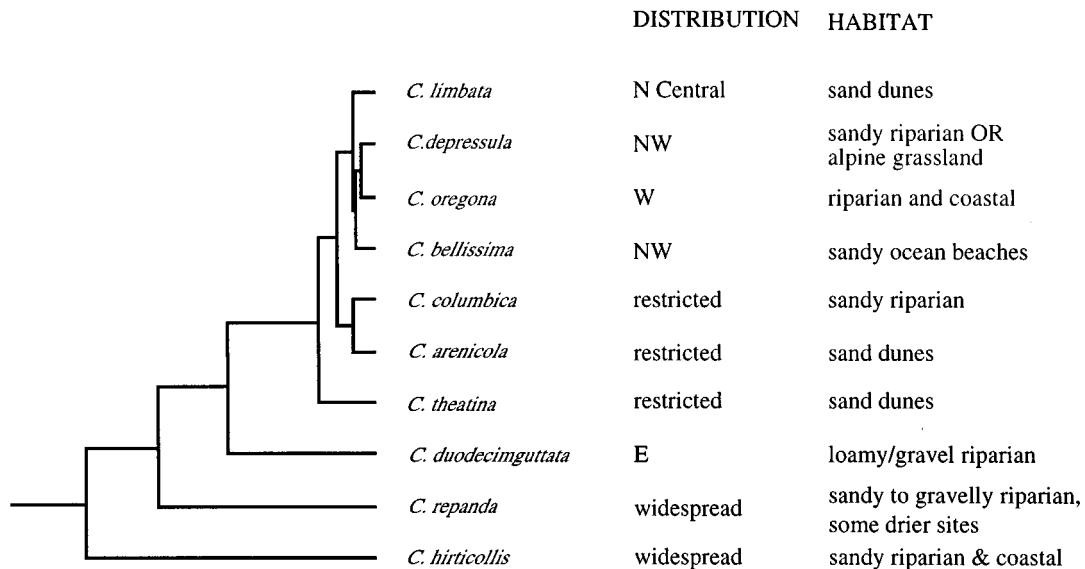


Figure 4. Phylogeny, distributional and habitat data for the 'repananda clade' of tiger beetles (genus: *Cicindela*).

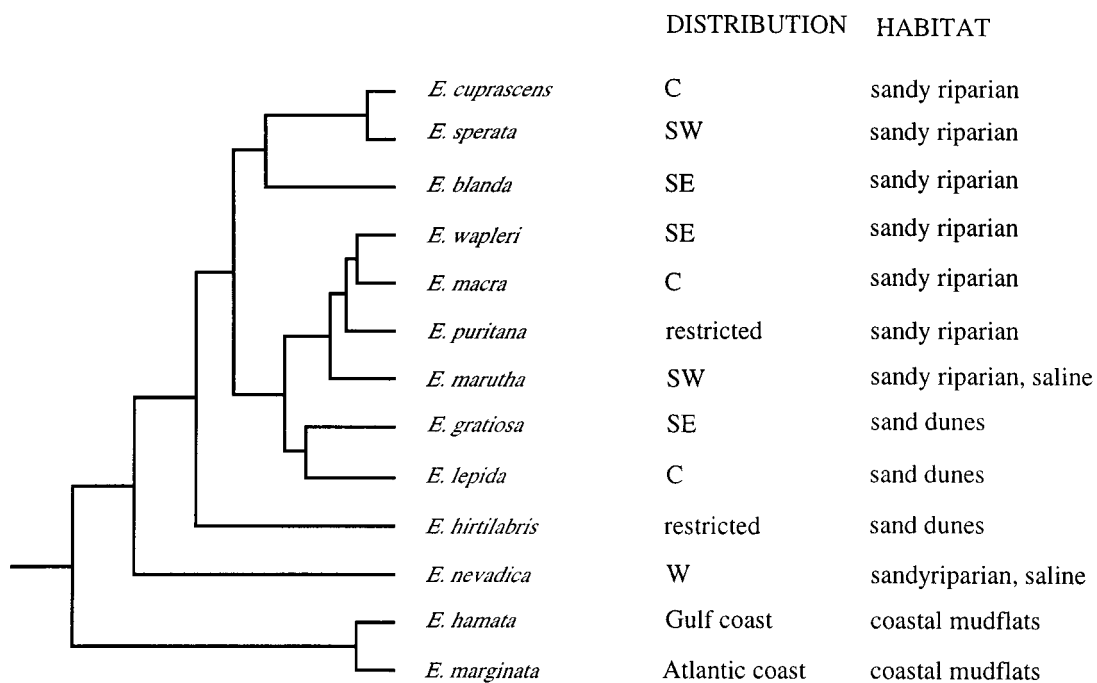


Figure 5. Phylogeny, distributional and habitat data for the *Ellipsoptera* clade of tiger beetles (genus: *Cicindela*).

two lineages of North American tiger beetles from the genus *Cicindela*. The 'repananda clade' is a lineage of ten species from the subgenus *Cicindela*, the North American radiation of a group found widely distributed across the Holarctic and more northerly latitudes (figure 4). The subgenus *Ellipsoptera* is a group of 13 species restricted to more central and southern areas of the USA, although the two lineages overlap widely in their distributions (figure 5). Both lineages comprise species living predominantly in sandy habitats, mostly associated with streams and riverbanks. However, both groups also include species living on sand dunes well away from water and species living on ocean beaches (Freitag 1965; Graves & Pearson 1973). Phylogenies of these species were

reconstructed using DNA sequence data, described in detail elsewhere (Vogler *et al.* 1998).

The plots of range sympatry against node height are shown in figures 6 and 7. In the *Ellipsoptera*, 8 out of 11 splits display little or no sympatry between sister clades, suggesting a pattern of strong vicariance with little subsequent range movement. Interestingly, there are replicated patterns of vicariance between different sublineages of *Ellipsoptera* apparently associated with drainage basins; splits associated with each side of the Appalachians have occurred three times, and splits associated with the Rio Grande versus Mississippi Drainage basin have occurred twice (Barraclough & Vogler 1998). Three of the older splits are characterized by sister clades with widely

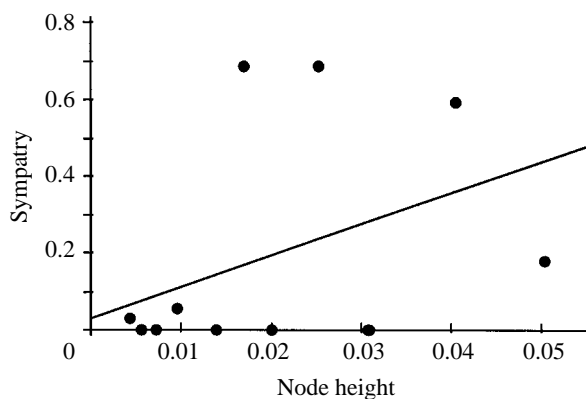


Figure 6. Relationship between the degree of sympatry and node height in the *Ellipsoptera* clade.

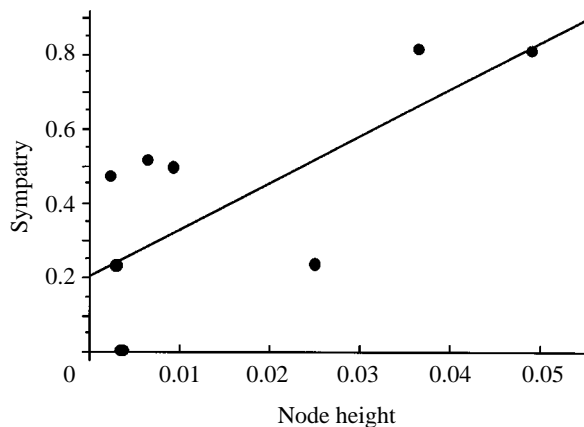


Figure 7. Relationship between the degree of sympatry and node height in the 'repanda clade'.

overlapping distributions, raising the issue of what features may be associated with this overlap in an otherwise predominantly allopatric group.

In the 'repanda clade' we observe a gradual increase in sympatry with node height, although with marked scatter about the line such that some quite recent splits are characterized by 50% range overlap. This pattern is consistent with expectations under the model of allopatric speciation followed by range changes outlined above, although we cannot rule out the possibility that ranges may have changed so much as to be effectively random with respect to phylogeny (the null model outlined above). Therefore, all we can say with certainty is that we observe strong evidence for post-speciational range changes in this group.

#### (b) *The relationship between phenotypic variation and species ranges*

Species differ phenotypically in many respects including morphology, ecology, behaviour, life history and sexual characteristics. These differences are the focus of the ecological perspective of species, and there is a large literature on the possible role of differences among species in promoting and maintaining species-richness (Brown & Wilson 1956; Hutchinson 1959; Strong *et al.* 1984; Martin 1996; Saetre *et al.* 1997). But do these phenotypic differences evolve in association with any of the stages of species accumulation, or do they arise arbitrarily with respect to the build-up of species-richness? One approach

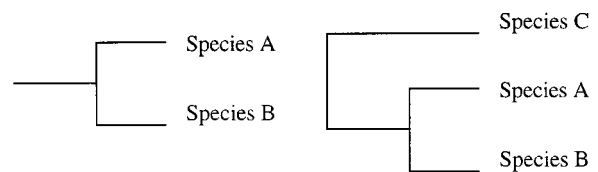


Figure 8. Calculation of habitat contrasts. (a) Sister species: if A and B have the same habitat type, contrast = 0; if A and B have different habitat types, contrast = 1. (b) Higher nodes: if C has same habitat as A and B, contrast = 0; if C has same habitat as either A or B, but not both, contrast = 0.5; if C has different habitat to both A and B, contrast = 1.

to this question is to partition phenotypic variation among nodes within the phylogeny, in the form of contrasts (Felsenstein 1985; Harvey & Pagel 1991). From this we can identify where phenotypic variation arose during the radiation of the group.

We use this to investigate the relationship between phenotypic changes and geography. As before, we consider the degree of sympatry between sister clades. There are three possible relationships between phenotypic contrasts and the degree of sympatry. First, there may be a positive relationship, which may be expected if phenotypic differences are necessary for sympatric species to coexist (Taper & Case 1992; Butlin 1995). Second, there may be a negative relationship, which may be expected if phenotypic variation evolves as a consequence of geographical variation in environmental conditions. Third, there may be no relationship if phenotype evolves at random with respect to sympatry.

We look at the origin of habitat differences among species in the two lineages of tiger beetles described above. Habitat contrasts were calculated from habitat data as shown in figure 8. Note that we plot rates of habitat change (i.e. scaled with respect to branch length), but that the same general patterns are observed with unscaled habitat contrasts. The plots of habitat contrasts against the degree of sympatry are shown in figures 9 and 10. In the *Ellipsoptera* there is a positive relationship, such that the origin of sympatry at higher levels within the phylogeny is associated with habitat differences, suggesting habitat differences may play a role in species coexistence in this lineage. In contrast, in the 'repanda clade' there is a negative relationship, such that sympatric sister clades are more likely to occupy similar habitats. This observation suggests these species have less fixed habitat requirements, and that observed habitat type may be simply a consequence of the opportunities available to species in the area they are found.

In summary, our analyses of species-level phylogenies in two lineages of tiger beetle provide the following results. First, the *Ellipsoptera* lineage displays a strong pattern of vicariance (non-overlapping ranges), whereas the 'repanda clade' has undergone more post-speciational range changes. Second, habitat differentiation is associated with sympatry between higher clades in *Ellipsoptera*, whereas in the 'repanda clade' it appears to be associated with differences in local opportunities between different areas. Having discovered these significant patterns, future work is necessary to explain the observed differences between the two lineages. Possible explanations

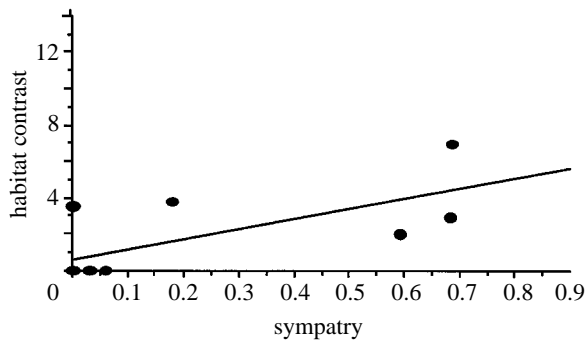


Figure 9. The relationship between habitat contrast and the degree of sympatry in the *Ellipsoptera*.

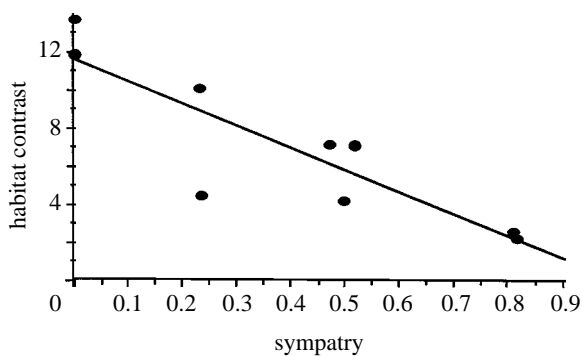


Figure 10. The relationship between habitat contrast and the degree of sympatry in the 'repanda' clade.

include differences in the environment experienced by each lineage, intrinsic differences in the rate of range changes over time, or intrinsic differences in the strength of current processes maintaining vicariant patterns, such as interspecific competition. Detailed analysis and discussion of the radiation of these tiger beetles will be presented elsewhere (Barraclough & Vogler 1998).

In conclusion, species-level phylogenies can provide information for testing ideas about the evolution of species-richness within groups. Future general application of this approach requires detailed simulation analysis of expected patterns under alternative scenarios, and publication of a sufficient number of suitable phylogenies to test these ideas.

#### 4. GENERAL CONCLUSIONS

Phylogenies provide an estimate of the the sequence of events leading to present-day patterns of species-richness and so provide indispensable information towards understanding the processes operating during the evolution of diversity (Cracraft 1981; Doyle & Donoghue 1993; Mooers & Heard 1997; Purvis 1996). We have outlined some ways in which this information may be used, and in this final section suggest some possible future developments in this area.

In §2 we described how sister-group comparisons provide replicate evidence for correlates of species-richness, allowing tests of whether intrinsic, biological factors may influence net rates of cladogenesis. This approach has already provided evidence supporting several long-standing hypotheses, but several future developments can be expected. First, similar methods may be used to

perform multivariate analyses to investigate what combination of factors explains variation in species-richness between clades, perhaps assessing the relative roles of biological and environmental factors in determining species-richness. Second, most currently available large phylogenies are complete to a particular higher taxonomic level, such as tribe or family, and so sister taxa are chosen at that level to maximize sample size. With the appearance of large phylogenies complete to the species-level (for example, Purvis 1995; Bininda-Emonds *et al.* 1998), it will become possible to localize changes in trait values and/or diversification rates to specific nodes in the phylogeny and thereby to compare sister groups at the point where changes relevant to the hypothesis occurred. Methods for localizing changes in diversification rate already exist (Sanderson & Donoghue 1994, 1996; Nee & Harvey 1994) but have not currently been used on a replicate basis to identify correlates of diversity, rather to detect shifts in diversification rate during the evolution of a single clade (Sanderson & Wojciechowski 1996; Vogler & Barraclough 1998).

In §3 we discussed possible uses of species-level phylogenies to investigate processes operating during the radiation of clades. To date, the relative paucity of suitable phylogenies for implementing these methods means that many studies of this kind take a specific, historical approach, for example, relating vicariant events in a clade's history to a particular historical environmental event (for example, Linder & Crisp 1995; Brumfield & Capparella 1996; Collins *et al.* 1996). But the current explosion of sequence data is providing the first opportunities to investigate general patterns of diversification across a range of taxa. Careful simulation studies will be necessary to interpret these patterns. In particular, we need to know: (i) what processes do leave a unique, detectable trace among extant species; (ii) how subsequent evolution and range changes among species influence our ability to detect past processes; and (iii) how sensitive are the methods to errors in phylogeny.

In conclusion, there will always be a limit to the certainty with which we can reveal the factors promoting speciation and species-richness, but with careful consideration of expected patterns under alternative scenarios, guided by phylogeny, we can gain some genuine empirical understanding of how species-richness and diversity evolves.

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#### REFERENCES

- Allmon, W. D. 1992 A causal analysis of stages in allopatric speciation. In *Oxford surveys in evolutionary biology* (ed. D. Futuyma & J. Antonovics), pp. 219–257. Oxford University Press.
- Barraclough, T. G. & Vogler, A. P. 1998 The molecular phylogeny and radiation of North American tiger beetles, genus *Cicindela* (Coleoptera: Cicindelidae).
- Barraclough, T. G., Harvey, P. H. & Nee, S. 1995 Sexual selection and taxonomic diversity in passerine birds. *Proc. R. Soc. Lond. B* **259**, 211–215.

- Barraclough, T. G., Harvey, P. H. & Nee, S. 1996 Rate of *rbcL* gene sequence evolution and species diversification in flowering plants (angiosperms). *Proc. R. Soc. Lond. B* **263**, 589–591.
- Barraclough, T. G., Nee, S. & Harvey, P. H. 1998 Sister-group analysis in identifying correlates of diversification. *Evol. Ecol.* (In the press.)
- Bininda-Emonds, O. R. P., Gittleman, J. L. & Purvis, A. A. 1998 Complete phylogeny of extant Carnivora (Mammalia). *Zoo. J. Linn. Soc.* (Submitted.)
- Bromham, L., Rambaut, A., & Harvey, P. H. 1996 Determinants of rate variation in mammalian DNA sequence evolution. *J. Molec. Evol.* **43**, 610–631.
- Brown, W. L. Jr & Wilson, E. O. 1956 Character displacement. *Syst. Zool.* **5**, 49–64.
- Brumfield, R. T. & Capparella, A. P. 1996 Historical diversification of birds in northwestern South America: a molecular perspective on the role of vicariant events. *Evolution* **50**, 1607–1624.
- Bullini, L. 1994 Origin and evolution of animal hybrid species. *Trends Ecol. Evol.* **2**, 8–13.
- Bush, G. L. 1969 Sympatric host race formation and speciation in frugivorous flies of the genus *Rhagoletis* (Diptera: Tephritidae). *Evolution* **23**, 237–251.
- Butlin, R. K. 1995 Reinforcement: an idea evolving. *Trends Ecol. Evol.* **10**, 432–434.
- Chase, M. W. (and 41 others) 1993 Phylogenetics of seed plants: an analysis of nucleotide sequences from the plastid gene *rbcL*. *Ann. MO Bot. Gdn* **80**, 528–580.
- Chesser, R. T. & Zink, R. M. 1994 Modes of speciation in birds: a test of Lynch's method. *Evolution* **48**, 490–497.
- Collins, T. M., Frazer, K., Palmer, A. R., Vermeij, G. J. & Brown, W. M. 1996 Evolutionary history of northern hemisphere *Nucella* (Gastropoda, Muricidae): molecular, morphological, ecological, and paleontological evidence. *Evolution* **50**, 2287–2304.
- Connor, E. F. & Taverner, M. P. 1997 The evolution and adaptive significance of the leaf-mining habit. *Oikos* **79**, 625.
- Coyne, J. A. 1992 Genetics and speciation. *Nature* **355**, 511–515.
- Cracraft, J. 1981 Patterns and process in paleobiology: the role of cladistic analysis in systematic paleontology. *Paleobiology* **7**, 456–458.
- Cracraft, J. 1985 Biological diversification and its causes. *Ann. MO Bot. Gdn* **72**, 794–822.
- Cracraft, J. 1990 The origin of evolutionary novelties: pattern and process at different hierarchical levels. In *Evolutionary innovations* (ed. M. H. Nitecki), pp. 21–44. University of Chicago Press.
- Darwin, C. 1871 *The descent of man and selection in relation to sex*. London: John Murray.
- Doyle, J. A. & Donoghue, M. J. 1993 Phylogenies and angiosperm diversification. *Paleobiology* **19**, 141–286.
- Ehrlich, P. R. & Raven, P. H. 1964 Butterflies and plants: a study in coevolution. *Evolution* **18**, 586–608.
- Farrell, B. D., Dussourd, D. E. & Mitter, C. 1991 Escalation of plant defense: do latex and resin canals spur plant diversification? *Am. Nat.* **138**, 881–900.
- Farrell, B. D. & Mitter, C. 1993 Phylogenetic determinants of insect/plant community diversity. In *Species diversity in ecological communities: historical and geographical perspectives* (ed. R. E. Ricklefs & D. Schluter), pp. 52–65. University of Chicago Press.
- Felsenstein, J. 1985 Phylogenies and the comparative method. *Am. Nat.* **125**, 1–15.
- Fisher, R. A. 1958 *The genetical theory of natural selection*. New York: Dover.
- Foote, R. H., Blanc, F. L. & Norrbom, A. L. 1993 *Handbook of the fruit flies (Diptera: Tephritidae) of America north of Mexico*. Ithaca, NY: Comstock.
- Freitag, R. 1965 A revision of the North American species of the *Cicindela maritima* group with a study of hybridization between *Cicindela duodecimguttata* and *oregona*. *Quest. Entomol.* **1**, 87–170.
- Gittleman, J. L. & Purvis, A. 1998 Body size and species-richness in carnivores and primates. *Proc. R. Soc. Lond. B* **265**, 113–119.
- Grant, V. 1981 *Plant speciation*. New York: Columbia University Press.
- Graves, R. C. & Pearson, D. L. 1973 The tiger beetles of Arkansas, Louisiana, and Mississippi (Coleoptera: Cicindelidae). *Trans. Am. Ent. Soc.* **99**, 157–203.
- Harvey, P. H. & Pagel, M. D. 1991 *The comparative method in evolutionary biology*. Oxford University Press.
- Harvey, P. H., May, R. M. & Nee, S. 1994 Phylogenies without fossils. *Evolution* **48**, 523–529.
- Harvey, P. H., Read, A. F. & Nee, S. 1995 Why ecologists need to be phylogenetically challenged. *J. Ecol.* **83**, 535–536.
- Hodges, S. A. & Arnold, M. L. 1995 Spurring plant diversification: are floral nectar spurs a key innovation? *Proc. R. Soc. Lond. B* **262**, 343–348.
- Hutchinson, G. E. 1959 Homage to Santa Rosalia, or why are there so many kinds of animals? *Am. Nat.* **93**, 145–159.
- Hutchinson, G. E. & MacArthur, R. H. 1959 A theoretical ecological model of size distributions among species of animals. *Am. Nat.* **93**, 117–125.
- Jablonski, D. 1987 Heritability at the species level: analysis of geographic ranges of Cretaceous mollusks. *Science* **238**, 360–363.
- Jackson, J. B. C. 1974 Biogeographic consequences of eurytopy and stenotopy among marine bivalves and their evolutionary significance. *Am. Nat.* **108**, 541–560.
- Kerr, J. T. & Packer, L. 1997 Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. *Nature* **385**, 252–254.
- Lande, R. 1981 Models of speciation by sexual selection on polygenic characters. *Proc. Natn. Acad. Sci. USA* **78**, 3721–3725.
- Linder, H. P. & Crisp, M. D. 1995 *Nothofagus* and Pacific biogeography. *Cladistics* **11**, 5–32.
- Lynch, J. D. 1989 The gauge of speciation: on the frequency of modes of speciation. In *Speciation and its consequences* (ed. D. Otte & J. A. Endler), pp. 527–553. Sunderland, MA: Sinauer Associates.
- Martin, T. E. 1996 Fitness costs of resource overlap among coexisting bird species. *Nature* **380**, 338–340.
- Mayr, E. 1954 Change of genetic environment and evolution. In *Evolution as a process* (ed. J. Huxley, A. C. Hardy & E. B. Ford), pp. 157–180. London: George Allen and Unwin.
- Mayr, E. 1963 *Animal species and evolution*. Cambridge, MA: Harvard University Press.
- McCall, R. A., Harvey, P. H. & Nee, S. 1998 Avian dispersal ability and the tendency to form island-endemic species on continental and oceanic islands. *Biodiv. Lett.* (Submitted.)
- Mindell, D. P. & Thacker, C. E. 1996 Rates of molecular evolution: phylogenetic issues and applications. *A. Rev. Ecol. Syst.* **27**, 279–303.
- Mitra, S., Landel, H. & Pruett-Jones, S. 1996 Species richness covaries with mating system in birds. *Auk* **113**, 544–551.
- Mitter, C., Farrell, B. & Wiegmann, B. 1988 The phylogenetic study of adaptive zones: has phytophagy promoted insect diversification? *Am. Nat.* **132**, 107–128.
- Mooers, A. Ø. & Heard, S. B. 1997 Evolutionary processes from tree shape. *Q. Rev. Biol.* **72**, 31–54.
- Mooers, A. Ø. & Møller, A. P. 1996 Colonial breeding and speciation in birds. *Evol. Ecol.* **10**, 375–385.
- Møller, A. P. & Birkhead, T. R. 1992 A pairwise comparative method as illustrated by copulation frequency in birds. *Am. Nat.* **139**, 644–656.
- Morse, D. R., Lawton, J. H., Dodson, M. & Williamson, M. H. 1985 Fractal dimension of vegetation and the distribution of arthropod body lengths. *Nature* **314**, 731–733.



- Nee, S. & Harvey, P. H. 1994 Getting to the roots of flowering plant diversity. *Science* **264**, 1549–1550.
- Nee, S., Holmes, E. C., May, R. M. & Harvey, P. H. 1994 Extinction rates can be estimated from molecular phylogenies. *Phil. Trans. R. Soc. Lond. B* **349**, 25–31.
- Nee, S., Barraclough, T. G. & Harvey, P. H. 1996a Temporal changes in biodiversity: detecting patterns and identifying causes. In *Biodiversity: a biology of numbers and difference* (ed. K. J. Gaston), pp. 230–252. Oxford: Blackwell Science.
- Nee, S., Read, A. F. & Harvey, P. H. 1996b Why phylogenies are necessary for comparative analysis. In *Phylogenies and the comparative method in animal behaviour* (ed. E. P. Martins), pp. 399–411. Oxford University Press.
- Orr, H. A. 1995 The population genetics of speciation: the evolution of hybrid incompatibilities. *Genetics* **139**, 1805–1813.
- Orr, H. A. & Orr, L. H. 1996 Waiting for speciation the effect of population subdivision on the time to speciation. *Evolution* **50**, 1742–1749.
- Panchen, A. L. 1992 *Classification, evolution and the nature of biology*. Cambridge University Press.
- Purvis, A. 1995 A composite estimate of primate phylogeny. *Phil. Trans. R. Soc. Lond. B* **348**, 405–421.
- Purvis, A. 1996 Using interspecies phylogenies to test macro-evolutionary hypotheses. In *New uses for new phylogenies* (ed. P. H. Harvey, A. J. Leigh Brown, J. Maynard Smith & S. Nee), pp. 153–168. Oxford University Press.
- Raup, D. M. 1985 Mathematical models of cladogenesis. *Paleobiology* **11**, 42–52.
- Raup, D. M., Gould, S. J., Schopf, T. J. M. & Simberloff, D. S. 1973 Stochastic models of phylogeny and the evolution of diversity. *J. Geol.* **81**, 525–542.
- Read, A. F. & Nee, S. 1995 Inferences from binary comparative data. *J. Theor. Biol.* **173**, 99–108.
- Ricklefs, R. E. & Schluter, D. 1993 *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press.
- Rosenzweig, M. L. 1995 *Species diversity in space and time*. Oxford University Press.
- Saetre, G. P., Moum, T., Bures, S., Kral, M., Adamjan, M. & Moreno, J. 1997 A sexually selected character displacement in flycatchers reinforces premating isolation. *Nature* **387**, 589–592.
- Sanderson, M. J. 1990 Estimating rates of speciation and evolution: a bias due to homoplasy. *Cladistics* **6**, 387–391.
- Sanderson, M. J. & Donoghue, M. J. 1994 Shifts in diversification rate with the origin of angiosperms. *Science* **264**, 1590–1593.
- Sanderson, M. J. & Donoghue, M. J. 1996 Reconstructing shifts in diversification rates on phylogenetic trees. *Trends Ecol. Evol.* **11**, 15–20.
- Sanderson, M. J. & Wojciechowski, M. F. 1996 Diversification rates in a temperate legume clade—are there so many species of *Astragalus* (Fabaceae). *Am. J. Bot.* **83**, 1488–1502.
- Sibley, C. G. & Ahlquist, J. E. 1990 *Phylogeny and classification of birds: a study in molecular evolution*. New Haven, CT: Yale University Press.
- Slatkin, M. 1996 In defense of founder-flush theories of speciation. *Am. Nat.* **147**, 493–505.
- Smith, J. L. & Bush, G. L. 1997 Phylogeny of the genus *Rhagoletis* (Diptera: Tephritidae) inferred from DNA sequences of mitochondrial cytochrome oxidase II. *Molec. Phylog. Evol.* **7**, 33–43.
- Southwood, T. R. E. 1973 The insect/plant relationship an evolutionary perspective. In *Insect-plant relationships* (ed. H. F. van Emden), pp. 3–30. London: Blackwell Scientific.
- Strong, D. R., Simberloff, D. S., Abele, L. G. & Thistle, A. B. 1984 *Ecological communities: conceptual issues and the evidence*. Princeton University Press.
- Taper, M. L. & Case, T. J. 1992 Coevolution among competitors. *Oxf. Surv. Evol. Biol.* **8**, 63–109.
- Templeton, A. R. 1996 Experimental evidence for the genetic transience model of speciation. *Evolution* **50**, 909–915.
- Vogler, A. P. & Barraclough, T. G. 1998 Reconstructing shifts in diversification rate during the radiation of tiger beetles (Cicindelidae). *Bulletino del Museo Turino*. (In the press.)
- Vogler, A. P., Welsh, A. & Barraclough, T. G. 1998 Radiation and molecular phylogeny of the *Cicindela maritima* group (Coleoptera: Cicindelidae) in North America. *Ann. Ent. Soc. Am.* (In the press.)
- West-Eberhard, M. J. 1983 Sexual selection, social competition and speciation. *Q. Rev. Biol.* **58**, 155–183.
- Wiegmann, B. M., Mitter, C. & Farrell, B. D. 1993 Diversification of carnivorous parasitic insects: extraordinary radiation, or specialized dead end? *Am. Nat.* **142**, 737–754.
- Zeh, D. W., Zeh, J. A. & Smith, R. L. 1989 Ovipositors, amnions and eggshell architecture in the diversification of terrestrial arthropods. *Q. Rev. Biol.* **64**, 147–168.

