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A tale of two analyses: estimating the consequences of shifts in hexapod diversification

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I present a novel descriptive (non-statistical) method to help identify the location and importance of shifts in diversification across a phylogeny. The method first estimates radiation rates across terminal higher taxa and then subjects these rates to a parsimony analysis across the phylogeny. The reconstructions define the magnitude, direction and influence of past shifts in realized diversification rates across nodes. I apply the method to data on the extant hexapod orders. The results indicate that the Coleoptera (beetles) and Diptera (flies) have contributed large upward shifts in diversification tendency, without which, under the model employed, global species richness would be reduced by 20% and 6%, respectively. The origin of Neoptera (insects with wing flexion), identified elsewhere as a significant radiation, may represent a large positive, a large negative or zero influence on current species richness, depending on the assumed phylogeny and parsimony method. The most influential radiations are attributable to the origin of the Eumetabola (insects with complete metamorphosis plus bugs and their relatives) and Pterygota (winged insects), but there is presently only weak evidence that they represent significant shifts in underlying diversification tendency. These analyses support some but not all results of previous phylogenetic analyses and the identity of the most important shift therefore remains elusive. New methodology involving comparisons across multiple taxa is likely to be necessary. © 2003 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2003, **80**, 23–36.

ADDITIONAL KEYWORDS: adaptive radiation – arthropod – diversity – insect – key innovation – macroevolution – phylogenetic tree shape – species richness.

INTRODUCTION

Which evolutionary events have given our planet its distinctive taxonomic signature? This question dominates the field of macroevolution (Stanley, 1979), a field that has received impetus from new phylogenies combined with methodology for extracting information about cladogenesis and extinction (see Harvey *et al.*, 1991; Nee, May & Harvey, 1994; Heard & Hauser, 1995; Nee, Barraclough & Harvey, 1996; Purvis, 1996; Sanderson & Donoghue, 1996; Mooers & Heard, 1997; Paradis, 1998; Nee, 2001).

The majority of new macroevolutionary studies have tested associations between repeatedly evolved traits and their effects on rates of cladogenesis (see Barraclough, Vogler & Harvey, 1999). Such studies are motivated partly by the need for statistical rigour in determining the causes of macroevolutionary events, which repeated evolutionary events allow. However such studies in themselves may fail to include the most important macroevolutionary events. The majority of extant species have probably resulted from relatively few extremely influential radiations, a fact implied by the 'hollow curve' nature of ranked plots of the species richness of higher taxa (see Williams, 1964; Mooers & Heard, 1997). For such radiations, three fundamental questions may be asked. First, do they represent true changes in the underlying rate of diversification? Second, are they important in a macroevolutionary sense? Third, what caused them? Though the first and third questions are commonly addressed in the literature, answers to the second have not been rigorously attempted. In this paper I address the second question in relation to hexapod diversification.

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The most sizeable radiations in the history of life are likely to have occurred amongst the Metazoa. Animals make up about 75% of described macroscopic species (Southwood, 1978), but most animal phyla contain very few species. The arthropods make up the vast majority of animal species and can be considered a significant radiation amongst metazoan phyla (Nee *et al.*, 1996). In turn the bulk of arthropod species are from the superclass Hexapoda (insects and their six-legged relatives) constituting about 57% of described macroscopic species. At least five events in hexapod evolution are commonly cited as being of macroevolutionary importance: the origin of the Insecta (insects), Pterygota (winged insects), Neoptera (insects with wing flexion), Holometabola (insects with complete metamorphosis) and Coleoptera (beetles) (e.g. Hutchinson, 1959; Evans, 1984; Carpenter & Burnham, 1985; Carpenter, 1992; Gullan & Cranston, 2000; Yang, 2001). In a previous study (Mayhew, 2002) I used nested sister-clade comparisons across the hexapod phylogeny (see Nee & Harvey, 1994; Nee *et al.*, 1996) to investigate if these and other groups represent significant shifts in diversification tendency. I showed that the Neoptera (or a slightly less inclusive group) probably do, whilst the Insecta, Pterygota, and Holometabola probably do not. In addition the Coleoptera and Diptera (flies) have probably diversified faster than their sister groups. The question here is: what was the macroevolutionary impact of these different shifts?

To evaluate the impact of shifts in diversification on present species richness, we need first to establish the magnitude and direction of the changes involved across nodes. However, it is often unclear if a significant difference between two taxa results from an increase in the diversity of one taxon, a decrease in the diversity of the other, or both. Comparisons with an outgroup are necessary to distinguish these hypotheses. Sophisticated maximum likelihood procedures (Sanderson & Donoghue, 1994), as well as nested sister-taxon comparisons (see Nee & Harvey, 1994; Nee *et al.*, 1996), can potentially distinguish the alternatives in the context of three-taxon phylogenies, which are the simplest and most tractable case. However, using only three taxa is restrictive when more phylogenetic information is available for either the ingroups or outgroup, because that information allows more accurate estimates of radiation rates along the branches in question. In the context of very comprehensive (e.g. dated species level) phylogenies, powerful likelihood methods are available that can identify radiations across the whole tree (Nee *et al.*, 1994; Purvis, Nee & Harvey, 1995). However, the necessary phylogenetic information is often absent.

In contrast, in many cases a phylogeny may be of intermediate completeness, such that relationships may be estimated for many taxa, and yet the terminal taxa are still inclusive higher taxa, within which the timing of branching events is unknown. In such cases we would like an analysis to make use of the whole of the available phylogenetic information. In a study of platyhelminth diversification, Brooks & McLennan (1993) applied parsimony analysis to species-richness data across a phylogeny of several higher taxa, and used the reconstruction to help localize shifts in diversification on the tree. The method is non-statistical, in that it is not based on a null model and cannot estimate the significance of shifts, but such reconstructions may be used in concert with other methods to increase understanding. Here I use a similar method to explore the magnitude and effects of realized changes in hexapod diversification. Instead of analysing species richness across the tree, as Brooks & McLennan (1993) did, I first calculated rates of diversification for terminal higher taxa by incorporating information on taxon age. I then estimated ancestral diversification rates by parsimony. The reconstructions define the magnitude and effects of shifts in rate across nodes. I thus ask the question, which events in hexapod evolution have been the most important? To my knowledge, this is the first study to attempt a rigorous answer to the question.

METHODS

ESTIMATING DIVERSIFICATION AT TIPS

The rate of diversification of terminal (phylogenetic-tip) taxa was calculated as $\ln(N)/t$ where N is current species richness and t is the time since origin (Myr). This assumes that diversification acts as a pure birth process such that the growth of the clade is exponential. The rate of diversification is both a realized average and a maximum likelihood estimate of probabilistic tendency under the stochastic 'Yule' birth process (Yule, 1924), in which the probability of a lineage branching follows a Poisson distribution. This is the simplest (single parameter) model of clade growth in common use (Sanderson & Donoghue, 1996). It allows simple yet meaningful statements about macroevolution when phylogenetic information is not very detailed, for example when the tips are all higher taxa (Purvis, 1996). Although the assumption that extinction does not occur is clearly false (though perhaps more appropriate for insects than for many other organisms), it does minimize assumptions in the face of uncertainty about which other (more complex) model of radiation might be the most appropriate. In addition, if we are to ask a single parameter question about radiation ('Which hexapods radiate the fastest?'), a single parameter model is an appropriate basis for a first response.

Species richnesses for higher taxa (mainly orders) came mainly from Parker (1982) and are presented in table 2 of Mayhew (2002). Parker (1982) is the most recently completed concurrent inventory of all major living taxa. Values are estimates of described species only. Whilst ignorance of the total number of species, described and undescribed, is frustrating in any study of speciose taxa, estimating undescribed species in this case introduces new assumptions and sources of error. Thus, I restrict conclusions to the picture that described species present, with all appropriate caution.

To estimate taxon age I used values for higher taxa from Ross & Jarzembowski (1993), also in table 2 of Mayhew (2002). Values are the mid-point of the age range of the earliest stratum from which the taxon was definitely recovered. Ignoring earlier possible strata makes these estimates conservative. I modified the estimates of taxon age by making a simple logical step based on phylogenetic relatedness: that sister taxa are the same age (whilst at the same time there is no equivalent phylogenetic restriction on taxon age for non-sister taxa). However, the ages of earliest known fossils often differ for sister taxa. Given that we are forced to assume for each analysis that the phylogeny used is correct, this discrepancy was treated as the result of incompleteness of the fossil record, and both sister taxa were assigned the age of the oldest of the pair. Another possibility exists, however: that the most recent earliest fossil is the true age of both and that earlier fossils in one clade are actually stem groups that have been misidentified. Whilst we cannot absolutely rule out such a possibility, awareness amongst palaeoentomologists should reduce its likelihood and has resulted in taxonomic revision (Hennig, 1981). Incompleteness of the arthropod fossil record is well established (e.g. Wills, 2001). Because the identity of the sister group of the hexapods remains enigmatic (Blaxter, 2001), I took the age of the hexapods to be that of the earliest hexapod fossil. For recent evidence on the true age of the hexapods see Gaunt & Miles (2002).

ESTIMATING DIVERSIFICATION ON INTERNAL NODES

A range of methods have been developed for estimating ancestral states of continuous characters across a phylogeny (see Webster & Purvis, 2002). Of the available methods most cannot be used in this context because their assumptions of evolutionary change along branches contradict the requirement here that states should change exclusively at nodes. The latter requirement derives from the fact that the estimates of states at tips are in fact average states over the time since taxa last shared an ancestor with other terminal taxa in the phylogeny. Two methods that do satisfy the requirement are linear parsimony and (unweighted) squared-change parsimony. Linear parsimony minimizes overall change in the character across the phylogeny using an algorithm of Swofford & Maddison (1987). The second method yields the set of ancestral states which minimizes squared change along branches. In both methods, the magnitude of change is independent of the length of branches, which is consistent with the requirement here that change occurs only at speciation events (nodes). Both methods were implemented in MacClade 4 (Maddison & Maddison, 2001). For linear parsimony, the estimated ancestral state sometimes included a range of possible values, in which case the mean was taken. For any internal node, the estimated rates allow one to calculate the expected species richness of the clade below the node at the time of the node. It should be stressed that these methods cannot identify significant changes in diversification tendency, merely changes in realized average rate. However, given that significant shifts have already been detected for the clades involved using other methods (Mayhew, 2002), the current methods are useful in assessing their magnitude and impact.

PHYLOGENETIC TOPOLOGY

I used several estimates of phylogenetic topology to take into account the extent of uncertainty in this, and estimated rates of diversification at both tips and internal nodes for each of them. The most recent and extensive estimate is that of Wheeler *et al*. (2001), and I used the tree given in their abstract (Fig. 1a). Since their study may not be definitive in the long term, and is open to potential criticism (Huelsenbeck, 1997), three other established estimates that incorporate all the current taxa were used: those of Kristensen (1995), Boudreaux (1979), and Hennig (1969) (Fig. 1B–D). These estimates cover the range of current opinion. Since the neuropteroid orders (lacewings and their relatives) are often treated as one taxon due to poor phylogenetic resolution, I also treated them as a single taxon. I did the same for the Phthiraptera (lice) + Psocoptera (booklice) (Psocodea), because the Psocoptera are probably paraphyletic. I omitted the newly described Mantophasmatodea (Klass *et al*., 2002) since their phylogenetic relations are uncertain and none of the above phylogeny estimates include them. I used orders as tips for the phylogenetic analysis in all other cases, assuming monophyly of each. Since linear parsimony cannot be used when the tree is not fully dichotomous, it was only used on the estimates of phylogeny that are (Boudreaux, 1979; Wheeler *et al*., 2001). Taxonomic definitions used throughout are as in Wheeler *et al*. (2001).

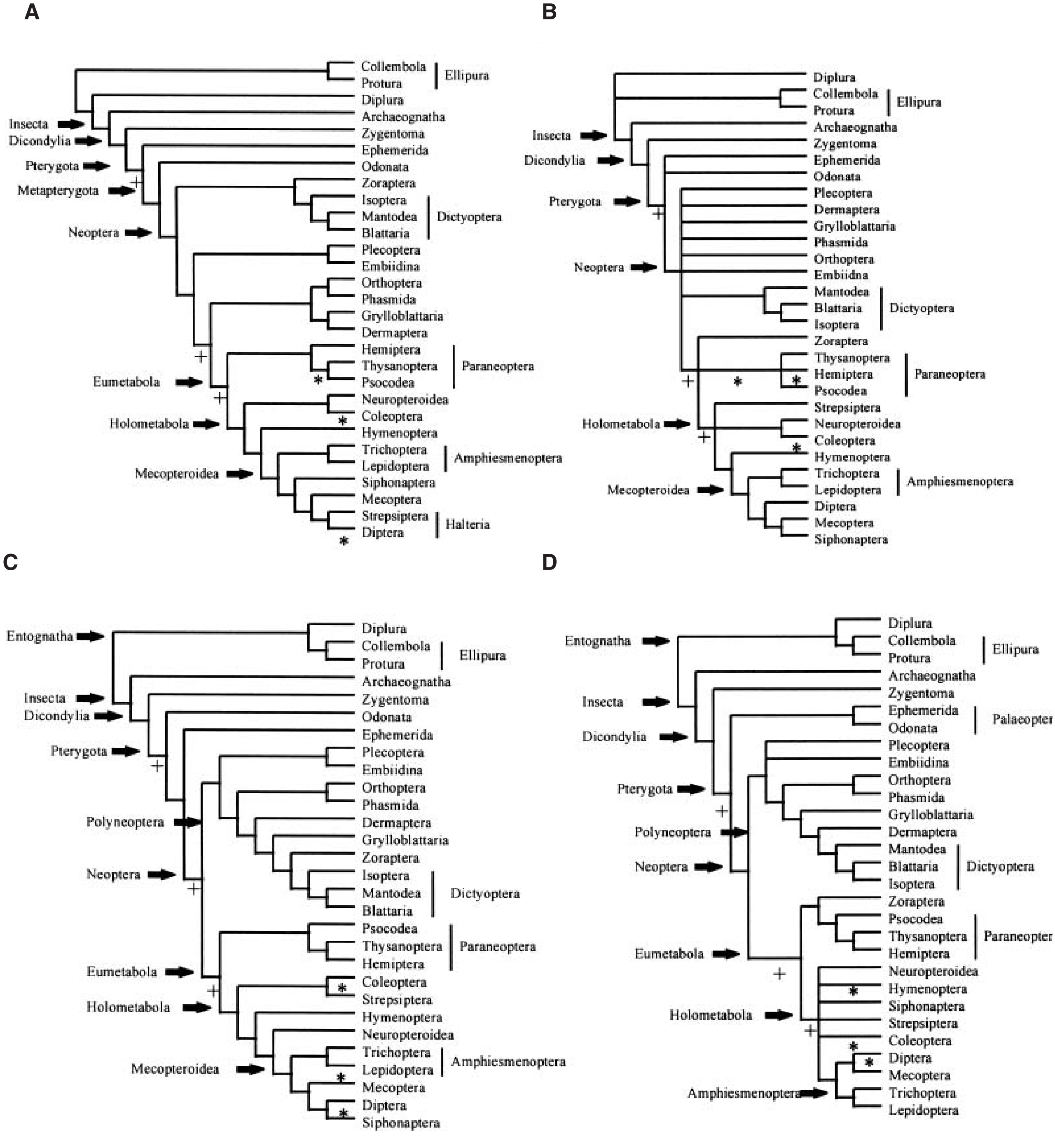

Figure 1. Phylogenetic relations of the extant hexapod orders according to (A) Wheeler *et al*. (2001), (B) Kristensen (1995), (C) Boudreaux (1979) and (D) Hennig (1969). Other higher taxa mentioned in the text are also shown (arrows indicate points of origin). Common names of orders are given in Table 1. The three largest increases in diversification rate (Table 1) are marked by *, whilst the three shifts with the largest positive effect (Table 2) are marked +. Marks are under the branch whose origin marks the shift.

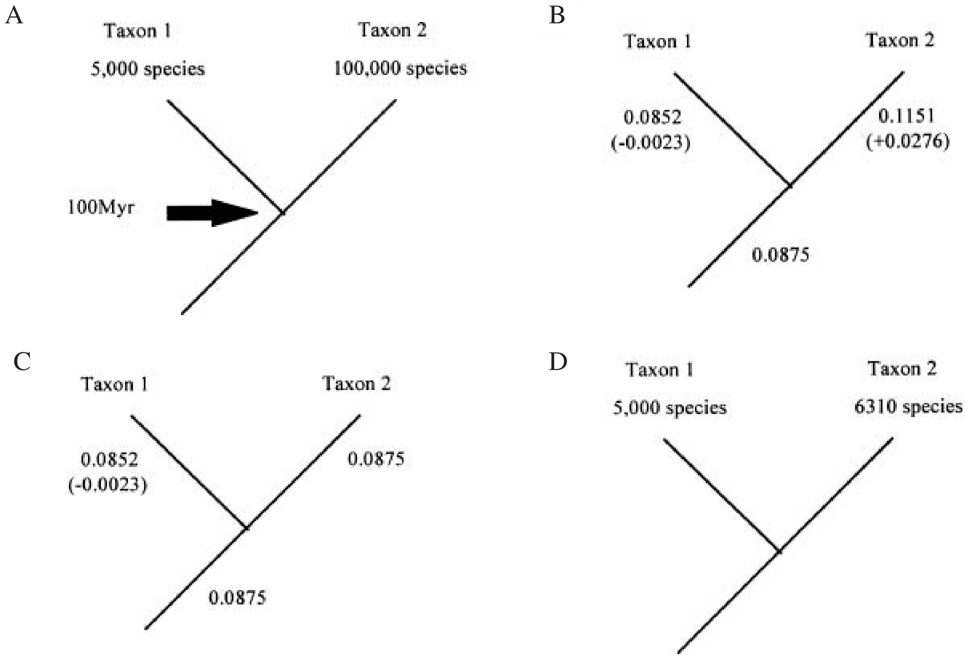

Figure 2. Estimation of shifts in diversification rates across nodes and their effects on extant species richness. (A) Imagine two sister taxa, 1 and 2, which contain 5000 and 100 000 species, respectively, (N) and which are estimated to be 100 Myr old (t). Their net rates of diversification ($\ln(N)/t$) are 0.0852 and 0.1151 Myr^{-1}, respectively. (B) Suppose, after applying a parsimony algorithm, that their ancestor is estimated to have radiated at 0.0875 Myr^{-1}. The differences between the rates of diversification of the two taxa and their common ancestor define the shifts across the node $\delta R = -0.0023$ and +0.0276, respectively. (C) Suppose now that history had been different and that the shift at the origin of taxon 2 had not occurred. It would then have radiated at the same rate as its ancestor ($r = 0.0875\ \mathrm{Myr}^{-1}$). (D) Radiating at that rate for 100 Myr would produce $e^{rt} = 6310$ species. The difference, δn, between this and the true species richness of taxon 2 is 93 690 species. Therefore 93 690 species is the effect of the shift.

ASSESSING THE EFFECT OF CHANGES AT NODES

To assess the impact of a historical change in the rate of diversification, we need to ask what would have occurred in its absence and compare that with observed species richness. The importance of the change can be assessed by the magnitude of the difference. There are several possible methods of estimating what would have occurred, but for present purposes shifts in rate are assumed to be independent and additive. This is necessary so that the effects of each shift are distinguishable from others, especially from subsequent shifts. To estimate the species-richness effects of a shift at a node, δn, the total radiation rate of the clade above the node was calculated as before [$\ln(N)/t$, where N is current species richness and t is the time since origin (Myr)] and then discounted by the size of the increase in shift at the node (δR) to get r, the diversification rate in the absence of the shift. The effect, δn, of δR is equal to present species richness, N, minus e^{rt}. Thus, $\delta n = N - e^{rt}$ where $r = [\ln(N)/t] - \delta R$. An example calculation is illustrated in Figure 2. Note that whilst shifts in rate were treated as additive, their effects on species richness are not additive. Thus we cannot assign an absolute number of extant species to each past shift in diversification. What we can do is postulate scenarios for the absence of each shift in isolation given that other shifts still occurred. Under these premises, shifts in diversification will have had greater impact if: (a) they involved large changes in rate; (b) they occurred in taxa that were already radiating rapidly or would subsequently radiate rapidly; (c) they occurred long ago.

As a gauge of the relative magnitude of any change, it is useful to have an estimate of described extant macroscopic planetary species richness. Southwood (1978) estimates 1 397 000 described species including 792 000 hexapods. The analyses in this paper assume 860 371 hexapods, so we can extrapolate roughly 1.5×10^6 described macroscopic species.

RESULTS

The estimated rate of diversification (Myr^{-1}) at the root of the hexapod tree was very similar across all trees and methods. It ranged from 0.0170 (Boudreaux tree, linear parsimony) to 0.0191 (Wheeler tree, linear parsimony).

Shifts in diversification rate (Myr^{-1}) across nodes ranged from 0.0219 (Coleoptera, Boudreaux tree, linear parsimony) to –0.0178 (Grylloblattaria (ice-crawlers), Wheeler tree, linear parsimony). Under linear parsimony, many nodes represented zero estimated shift in diversification and when shifts occurred they tended to be more extreme than they were under squared-change parsimony (Table 1).

Of those nodes that occur in all trees, the greatest average positive shifts occurred within the Coleoptera, Diptera, Lepidoptera (butterflies, moths), Orthoptera (grasshoppers, crickets) and Hymenoptera (sawflies, wasps, bees, ants) (Table 1). These are all large orders and substantially more species-rich than are other closely related orders. The greatest average negative shifts occurred in the Grylloblattaria, Zoraptera, Strepsiptera, Mecoptera (scorpionflies), Embiidina (webspinners), Protura and Trichoptera (caddisflies). These are substantially less species-rich than are other closely related orders. Of the commonly postulated supraordinal taxa, the largest upward shifts were indicated at the origin of the Eumetabola (insects with complete metamorphosis plus the Paraneoptera), the Paraneoptera (bugs and their relatives), and the Pterygota (Table 1). The origin of the Dicondylia (insects minus Archaeognatha) and Holometabola may have coincided with zero change in diversification rate, whilst the origins of the Neoptera and Insecta may actually have represented a decrease in diversification rate and consistently represent very small changes.

The shifts estimated to have had greatest positive influence on current species richness are the origin of the Eumetabola and Pterygota, each accounting for half a million extant species, and the Coleoptera, accounting for a third of a million (Table 2). The origin of the Holometabola and Dicondylia may have been very influential (Kristensen, Boudreaux and Hennig trees, squared-change parsimony) but may not have had any impact at all (linear parsimony analyses), whilst the Lepidoptera, Hymenoptera and Diptera are all consistently influential (about 10^5 species added).

The origin of the Neoptera may have accounted for half a million species (Boudreaux tree, squared-change parsimony) but may have caused a reduction of a quarter of a million species (Wheeler and Kristensen trees, squared-change parsimony). The origin of the insects is unlikely in itself to have had any significant impact (Table 2). The origin of several postulated higher taxa containing the small mecopteroid and polyneopterous orders are estimated to have had the highest negative impact on current species richness.

DISCUSSION

This study aimed to identify the macroevolutionary impact of previously identified shifts in hexapod diversification by comparisons across multiple taxa. It indicates that the evolution of the Coleoptera and Diptera both had a substantial positive impact on current species richness. It also confirms that the origin of the Insecta in itself is unlikely to have contributed much. However, contrary to previous studies, it indicates that although the origin of the Neoptera may have contributed a substantial number of species, it may also have been associated with a negative effect on diversification. Its origin is consistently associated with very little change in the rate of diversification. In addition, the shifts in realized diversification rate estimated to have had most macroevolutionary impact, the origin of the Eumetabola and Pterygota, were previously found not to represent significant shifts in diversification. Below I first discuss the implications of these results in the context of previous work, before going on to consider how they might be improved upon.

CANDIDATE INFLUENTIAL SHIFTS

The order Coleoptera has long held macroevolutionary interest amongst biologists because 20% of all described species belong to it and it is the most species-rich hexapod order, a fact that J.B.S. Haldane supposedly cited as revealing the Creator's 'inordinate fondness' (Hutchinson, 1959). Mayhew (2002) showed that the order has on average diversified faster than has its sister group. This study explicitly suggests that the group is also a radiation, in the sense that it represents an increase in the net rate of diversification compared to its ancestral branch, and furthermore that without the shift, the planet would indeed be about 20% less species-rich. Thus, the beetles have certainly had a large macroevolutionary impact. The work of Farrell (1998), however, suggests that their species richness is largely a consequence of radiations amongst derived beetle taxa, so the present quantitative result should be taken with some caution. The Diptera is another group representing a significant shift in diversification, but without the shift at their origin the planet would only be about 6% less species-rich. In both groups the search for key innovations is likely to prove fruitful.

The Insecta differ from the non-insect hexapods (Entognatha) in several synapomorphous morphological characteristics (13 according to Wheeler *et al.*, 2001). It has been argued that the acquisition of these characteristics was a prerequisite for their macroevolutionary success. Mayhew (2002) showed that despite their overall species richness, the origin of the Insecta likely did not represent a significant shift in diversification because the primitive insect lineages only diversified as fast as their non-insect relatives. This study confirms that finding in that the estimated magnitude of the shift in rate across the node is consistently small, and accounts for very little current diversity. Whatever the subsequent effects of the Insecta synapomorphies, in isolation they apparently made little macroevolutionary impact.

The Neoptera are characterized by several synapomorphies, including most notably wing flexion. Mayhew (2002) considered that the Neoptera most likely represented the most significant hexapod radiation. In this analysis the estimated shift at the origin of the group is consistently very small, the largest shifts in rate occuring instead nearer the tip of the tree. However, under one set of assumptions the shift does translate into a substantial effect on species richness thanks to the age of the group. The principal reason in this case seems to be the assumption of a monophyletic Polyneoptera. In the trees that assume this (Boudreaux, Hennig) the ancestral Neoptera are estimated to have diversified slightly faster because the very diverse Eumetabola form one immediate daughter lineage and hence are influential. In the trees that assume a paraphyletic or unresolved Polyneoptera (Wheeler, Kristensen), the very diverse Eumetabola are not an immediate daughter branch and have very little influence on the ancestral Neoptera. Instead, the immediate daughters are mostly species-poor groups, which imply that the origin of the Neoptera had small or negative effects on diversity.

These results show that when higher taxa comprise both species-rich and species-poor subtaxa, taking account of the relationships between these subtaxa can be very important when attempting to locate shifts in diversification. A high average tendency to diversify across the Neoptera as a whole, which led to significance in the pairwise comparisons (Mayhew, 2002), may be largely a consequence of subsequent radiations in much more derived taxa, particularly within orders, such that the shift across the node at the origin of the clade may not be great, and may even be negative. Such problems are difficult to identify in nested pairwise comparisons when subsequent shifts occur much later in the phylogeny. This study therefore casts doubt on the previous finding that the origin of the Neoptera represents a significant shift, and on the validity in general of analyses, aimed at locating shifts, that only incorporate a few higher taxa.

Similarly, the origins of the Eumetabola and Pterygota, which were previously only weakly indicated to be significant radiations, here are consistently associated with high positive shifts in diversification rate and have had an extremely large impact on modern species richness. Whilst a large absolute shift need not necessarily be a significant one, previously used pairwise tests of significance inherently lack power since they incorporate minimal data to estimate rates. Thus the data, although not currently indicating that the origins of these groups were significant radiations, also do not strongly refute that possibility. They suggest that more effort should be devoted to the possibility of key innovations at the origin of the Eumetabola, a neglected event in hexapod evolution.

The signal here about the origin of the Holometabola is ambiguous. Although it is never reconstructed as a negative macroevolutionary step, it is not always reconstructed as a large positive one. This is largely because the Paraneoptera are estimated to have high rates of diversification such that the more ancient origin of Eumetabola as a whole is usually of greater importance. Mayhew (2002) also concluded that the difference in diversity between the Paraneoptera and Holometabola was not sufficiently large to imply differences in the underlying rate of diversification. In contrast, a recent study based on fossil families (Yang, 2001) concluded that complete metamorphosis does represent a key innovation: that the Holometabola have had consistently higher rates of diversification than have their ancestors and sister groups, contributing to the bulk of insect diversity. Why the different result? There are several possibilities, including the different Linnean taxa involved (families by Yang, species here), the inclusion by Yang (but not here) of extinct taxa, the different underlying model of cladogenesis (linear radiation by Yang, exponential here), and the extent to which subsequent radiations are taken into account (radiations up to order level here, not by Yang). Both types of analysis have their advantages and drawbacks and in the long term ways need to be found to reconcile their different conclusions.

The results of this study also indicate that the origin of several taxa have limited the species richness of the planet to varying degrees. The Strepsiptera, Grylloblattaria, Zoraptera and Neuropteroidea are all significantly less species-rich than are related taxa (Mayhew, 2002), and all have limited planetary diversity relative to their ancestors. However, the magnitude of the reduction is always slight because their ancestral lineages probably did not diversify very rapidly either. With the notable exception of mass extinction events, the emphasis in macroevolutionary studies is normally on diversifying events. Results here emphasize that current diversity is a product both of positive shifts that have enhanced diversity and of negative shifts that have reduced it. Such downward shifts probably occur regularly in a range of taxa and should be the subject of equal interest.

IMPROVEMENTS

This study is a first attempt to identify the influence of shifts in diversification, and has posed as many

Table 1. Estimated shifts in diversification rate (δR) with the origin of higher hexapod clades under different assumptions

	Shift in diversification rate across node (Myr^{-1})							
Clade originating	Wheeler sq-ch	Wheeler linear	Kristensen sq-ch	Boudreaux sq-ch	Boudreaux linear	Hennig sq-ch	Mean	SE
Coleoptera (beetles)	0.0097	0.0138	0.0130	0.0156	0.0219	0.0129	0.0145	0.0017
Diptera (flies)	0.0137	0.0216	0.0056	0.0109	0.0149	0.0085	0.0125	0.0023
Thysanoptera + Psocodea	0.0082	0.0134	–	–	–	–	0.0108	0.0026
Lepidoptera (butterflies and moths)	0.0070	0.0077	0.0068	0.0077	0.0117	0.0077	0.0081	0.0007
Eumetabola	0.0078	0.0095	–	0.0048	0.0068	0.0025	0.0063	0.0012
Orthoptera (grasshoppers, crickets)	0.0043	0.0055	0.0091	0.0051	0.0069	0.0062	0.0062	0.0007
Hymenoptera (sawflies, wasps, bees, ants)	0.0024	0.0036	0.0056	0.0044	0.0094	0.0096	0.0058	0.0012
Hemiptera (bugs)	–0.0015	0.0000	0.0103	0.0067	0.0108	0.0080	0.0057	0.0021
Paraneoptera	0.0067	0.0062	0.0099	0.0017	0.0012	0.0080	0.0056	0.0014
Collembola (springtails)	0.0041	0.0033	0.0045	0.0045	0.0053	0.0045	0.0044	0.0003
Pterygota	0.0026	0.0044	0.0032	0.0037	0.0070	0.0032	0.0040	0.0006
Neuropteroidea + Coleoptera	0.0020	0.0000	0.0089	–	–	–	0.0036	0.0027
Dictyoptera	0.0039	0.0000	0.0014	0.0058	0.0074	0.0020	0.0034	0.0011
Plecoptera (stoneflies)	0.0040	0.0027	0.0020	0.0040	0.0044	0.0024	0.0032	0.0004
Eumetabola + Orthoptera + Phasmida + Grylloblattaria + Dermaptera	0.0045	0.0015	–	–	–	–	0.0030	0.0015
Neoptera minus (Zoraptera + Dictyoptera)	0.0037	0.0018	–	–	–	–	0.0028	0.0010
Diptera + Siphonoptera	–	–	–	0.0053	0.0000	–	0.0027	0.0027
Holometabola	0.0011	0.0000	0.0059	0.0031	0.0000	0.0057	0.0026	0.0011
Hemiptera + Thysanoptera	–	–	–	0.0026	0.0000	0.0051	0.0026	0.0015
Orthoptera + Phasmida	0.0018	0.0000	–	0.0033	0.0017	0.0054	0.0024	0.0009
Palaeoptera	–	–	–	–	–	0.0024	0.0024	–
Halteria	0.0047	0.0000	–	–	–	–	0.0024	0.0024
Dermaptera (earwigs)	0.0071	0.0015	0.0012	0.0021	0.0000	0.0021	0.0023	0.0010
Amphiesmenoptera	0.0024	0.0000	0.0020	0.0036	0.0016	0.0036	0.0022	0.0006
Odonata (dragonflies, damselflies)	0.0024	0.0010	0.0032	0.0023	0.0013	0.0026	0.0021	0.0003
Dermaptera + Dictyoptera	–	–	–	–	–	0.0021	0.0021	–
Blattaria (cockroaches)	0.0021	0.0019	0.0015	0.0025	0.0023	0.0016	0.0020	0.0002
Hymenoptera + Mecopteroidea	–0.0009	0.0000	0.0061	–	–	–	0.0017	0.0022
Eumetabola + Zoraptera	–	–	0.0017	–	–	–	0.0017	–
Metapterygota	0.0014	0.0016	–	–	–	–	0.0015	0.0001
Isoptera + Blattaria	–	–0.0011	–	–	0.0013	0.0012	0.0001	
Psocodea (lice, booklice)	0.0037	0.0009	0.0000	–0.0010	0.0005	0.0028	0.0012	0.0007
Mantodea + Blattaria	0.0019	0.0000	–	0.0026	0.0000	–	0.0011	0.0007
Coleoptera + Strepsiptera	–	–	–	0.0022	0.0000	–	0.0011	0.0011
Isoptera (termites)	0.0021	0.0000	0.0007	0.0032	0.0004	–0.0003	0.0010	0.0006
Dicondylia	0.0008	0.0000	0.0014	0.0015	0.0005	0.0013	0.0009	0.0002

Ephemerida + Neoptera	–	–	–	0.0014	0.0000	–	0.0007	0.0007
Polyneoptera minus (Plecoptera + Embiidina)	–	–	–	–	–	0.0005	0.0005	–
Hymenoptera + Mecopteroidea + Neuropteroidea	–	–	–	0.0009	0.0000	–	0.0005	0.0005
Neoptera	–0.0009	0.0000	–0.0008	0.0030	0.0004	0.0007	0.0004	0.0006
Diplura + Insecta	0.0006	0.0000	–	–	–	–	0.0003	0.0003
Ellipura	0.0005	0.0000	0.0002	0.0002	0.0000	0.0003	0.0002	0.0001
Diplura (diplurans)	0.0011	0.0014	–0.0006	–0.0006	0.0000	–0.0005	0.0001	0.0004
Insecta	–0.0006	0.0000	0.0005	0.0004	0.0002	0.0003	0.0001	0.0002
Mantodea (mantids)	–0.0002	–0.0004	0.0003	0.0002	0.0000	0.0006	0.0001	0.0001
Ephemerida (mayflies)	0.0013	0.0000	0.0007	–0.0016	0.0000	–0.0001	0.0001	0.0004
Mecopteroidea	–0.0033	–0.0005	0.0005	0.0003	0.0000	0.0020	–0.0002	0.0007
Entognatha	–	–	–	–0.0004	0.0000	–0.0004	–0.0003	0.0001
Plecoptera + Embiidina	–0.0009	0.0000	–	0.0008	0.0000	–	–0.0004	0.0002
Thysanoptera (thrips)	0.0037	0.0000	–0.0005	–0.0041	0.0000	–0.0028	–0.0006	0.0011
Phasmida (stick insects)	–0.0026	–0.0015	0.0028	–0.0018	0.0000	–0.0007	–0.0006	0.0008
Archaeognatha (bristletails)	–0.0015	–0.0019	–0.0009	–0.0012	0.0000	–0.0010	–0.0011	0.0003
Polyneoptera	–	–	–	–0.0018	0.0000	–0.0019	–0.0012	0.0006
Zoraptera + Dictyoptera	–0.0046	–0.0010	–	0.0003	0.0000	–	–0.0013	0.0011
Zygentoma (silverfish)	–0.0018	–0.0014	–0.0018	–0.0022	0.0000	–0.0018	–0.0015	0.0003
Mecoptera + Halteria	–0.0018	–0.0012	–	–	–	–	–0.0015	0.0003
Mecoptera + Diptera + Siphonaptera	–	–	0.0015	–0.0033	0.0000	–	–0.0016	0.0010
Orthoptera + Grylloblattaria + Phasmida + Dermaptera	–0.0033	0.0000	–	–	–	–	–0.0017	0.0017
Diptera + Mecoptera	–	–	–	–	–	–0.0018	–0.0018	–
Neuropteroidea + Mecopteroidea	–	–	–	–0.0035	–0.0002	–	–0.0018	0.0017
Grylloblattaria + Dermaptera	–0.0050	0.0000	–	–	–	–	–0.0025	0.0025
Siphonaptera (fleas)	–0.0038	0.0000	–0.0013	–0.0055	–0.0016	–0.0055	–0.0029	0.0010
Dermaptera + Dictyoptera + Grylloblattaria + Zoraptera	–	–	–	–0.0042	–0.0020	–	–0.0031	0.0011
Zoraptera + Paraneoptera	–	–	–	–	–	–0.0032	–0.0032	–
Neuropteroidea (lacewings, etc.)	–0.0076	0.0000	–0.0043	–0.0038	–0.0022	–0.0021	–0.0033	0.0011
Trichoptera (caddisflies)	–0.0047	–0.0040	–0.0049	–0.0040	0.0000	–0.0040	–0.0036	0.0007
Protura (proturans)	–0.0047	–0.0056	–0.0043	–0.0043	–0.0035	–0.0043	–0.0045	0.0003
Grylloblattaria + Dermaptera + Dictyoptera	–	–	–	–	–	–0.0050	–0.0050	–
Embiidina (webspinners)	–0.0049	–0.0062	–0.0052	–0.0049	–0.0046	–0.0048	–0.0051	0.0002
Grylloblattaria + Zoraptera + Dictyoptera	–	–	–	–0.0063	–0.0069	–	–0.0066	0.0003
Mecoptera + Siphonaptera	–	–	0.0072	–	–	–	–0.0072	–
Mecoptera (scorpionflies)	–0.0065	–0.0033	–0.0058	–0.0087	–0.0101	–0.0102	–0.0074	0.0011
Halteria + Siphonaptera + Mecoptera	–0.0056	–0.0111	–	–	–	–	–0.0084	0.0028
Strepsiptera (strepsipterans)	–0.0090	–0.0011	–0.0089	–0.0133	–0.0070	–0.0110	–0.0084	0.0017
Zoraptera (zorapterans)	–0.0086	–0.0146	–0.0142	–0.0056	–0.0069	–0.0111	–0.0102	0.0015
Grylloblattaria (ice-crawlers)	–0.0121	–0.0178	–0.0138	–0.0066	–0.0082	–0.0089	–0.0112	0.0017

For definitions of supra-ordinal clades, see Fig. 1. Phylogenetic relationships (see Fig. 1) according to Wheeler *et al*. (2001), Kristensen (1995), Boudreaux (1979) or Hennig (1969). Ancestral state estimation by squared-change parsimony (sq-ch), or linear parsimony (linear). Clades are in order of mean shift.

Table 2. Influence of shifts in hexapod diversification outlined in Table 1, as measured by influence on present species richness (δn)

	Species loss in absence of shift (*N*)							
Clade originating	Wheeler sq-ch	Wheeler linear	Kristensen sq-ch	Boudreaux sq-ch	Boudreaux linear	Hennig sq-ch	Mean	SE
Eumetabola	725 000	759 000	–	635 000	717 000	445 000	656 000	56 700
Pterygota	489 000	651 000	554 000	599 000	867 000	554 000	619 000	54 200
Neoptera minus (Zoraptera + Dictyoptera)	578 000	364 000	–	–	–	–	471 000	107 000
Eumetabola + Orthoptera + Phasmida + Grylloblattaria + Dermaptera	611 000	297 000	–	–	–	–	454 000	157 000
Eumetabola + Zoraptera	–	–	339 000	–	–	–	339 000	–
Metapterygota	313 000	347 000	–	–	–	–	330 000	17 000
Coleoptera	306 000	326 000	323 000	329 000	335 000	328 000	325 000	3 980
Holometabola	195 000	0	588 000	424 000	0	581 000	298 000	111 000
Dicondylia	197 000	0	314 000	331 000	129 000	296 000	211 000	52 800
Ephemerida + Neoptera	–	–	–	312 000	0	–	156 000	156 000
Neuropteroidea + Coleoptera	149 000	0	315 000	–	–	–	154 000	90 900
Lepidoptera	119 000	123 000	118 000	123 000	135 000	123 000	124 000	2 470
Hymenoptera	64 500	83 500	104 000	93 000	121 000	122 000	97 900	9 100
Diptera	96 600	99 500	79 800	93 300	97 500	91 200	93 000	2 900
Diplura + Insecta	179 000	0	–	–	–	–	89 700	89 700
Coleoptera + Strepsiptera	–	–	–	157 000	0	–	78 700	78 700
Hymenoptera + Mecopteroidea	–109 000	0	314 000	–	–	–	68 400	127 000
Paraneoptera	77 300	75 200	85 300	34 900	26 300	79 100	63 000	10 400
Amphiesmenoptera	73 600	0	64 500	95 200	53 000	90 900	62 900	14 100
Neoptera	–290 000	0	–253 000	529 000	104 000	173 000	43 800	124 000
Hymenoptera + Mecopteroidea + Neuropteroidea	–	–	–	87 300	0	–	43 700	43 700
Hemiptera	–37 800	0	74 400	65 800	75 000	69 800	41 200	19 700
Diptera + Siphonaptera	–	–	–	79 400	0	–	39 700	39 700
Halteria	74 200	0	–	–	–	–	37 100	37 100
Hemiptera + Thysanoptera	–	–	–	41 500	0	62 200	34 600	18 300
Insecta	–185 000	0	152 000	124 000	64 500	746	26 000	49 300
Dictyoptera	5 300	0	2 680	6 280	6 750	108 000	21 500	17 400
Ellipura	1 200	0	507	507	0	94 900	16 200	15 700
Orthoptera	13 300	14 900	17 600	14 400	16 200	15 600	15 300	601
Orthoptera + Phasmida	8 660	0	–	13 700	8 610	17 300	9 660	2 920
Thysanoptera + Psocodea	7 490	9 200	–	–	–	–	8 350	853
Collembola	5 200	4 720	5 390	5 390	5 690	5 390	5 300	132
Polyneoptera minus (Plecoptera + Embiidina)	–	–	–	–	–	4 420	4 420	–
Odonata	2 660	1 300	3 170	2 580	1 640	2 680	2 340	290
Isoptera + Blattaria	–	–	1 670	–	–	1 920	1 790	71.0
Blattaria	1 790	1 670	1 390	2 020	1 910	1 470	1 710	100

Plecoptera	1 260	985	922	1 260	1 320	3 830	1 600	451
Mantodea + Blattaria	2 480	0	–	3 080	0	–	1 390	812
Dermaptera	1 250	467	477	732	0	4 360	1 210	652
Palaeoptera	–	–	–	–	–	1 050	1 050	–
Psocodea	2 410	712	0	–1 670	687	2 920	843	679
Dermaptera + Dictyoptera	–	–	–	–	–	732	732	–
Isoptera	967	0	396	1 270	237	–198	445	231
Mantodea	–118	–243	163	111	0	312	37.0	81.8
Diplura	242	294	–213	–213	0	–174	–11.0	94.1
Ephemerida	745	0	440	–1 480	0	–67.0	–60.0	312
Archaeognatha	–178	–242	–96.1	–135	0	–109	–127	33.3
Zygentoma	–269	–195	–269	–353	0	–269	–226	49.5
Plecoptera + Embiidina	–652	0	–	–625	0	–	–319	184
Grylloblattaria	–247	–1 050	–1 020	–92.3	–159	–205	–462	182
Embiidina	–508	–790	–840	–508	–447	–716	–635	68.4
Zoraptera	–285	–2 030	–1 780	–98.0	–155	–330	–780	359
Phasmida	–2 850	–1 380	1 470	–1 730	0	–568	–842	612
Entognatha	–	–	–	–1 280	0	–1 280	–852	426
Protura	–1 070	–1 610	–885	–885	–592	–885	–988	139
Zoraptera + Dictyoptera	–24 700	–2 790	–	20 600	0	–	–1 730	9 260
Thysanoptera	2 120	0	–688	–9 390	0	–5 290	–2 210	1 750
Grylloblattaria + Dermaptera	–5 040	0	–	–	–	–	–2 520	2 520
Siphonaptera	–3 420	0	–783	–5 050	–814	–6 640	–2 780	1 100
Strepsiptera	–3 000	–114	–4 260	–8 150	–1 550	–8 060	–4 190	1 360
Mecoptera	–2 580	–746	–2 020	–5 240	–7 940	–8 310	–4 470	1 300
Neuropteroidea	–25 600	0	–8 750	–9 050	–3 910	–3 790	–8 520	3 690
Trichoptera	–15 800	–12 000	–17 000	–12 000	0	–12 000	–11 500	2 460
Mecoptera + Siphonaptera	–	–	–15 100	–	–	–	–15 100	–
Dermaptera + Dictyoptera + Grylloblattaria + Zoraptera	–	–	–	–25 100	–7 710	–	–16 410	8 700
Polyneoptera	–	–	–	–24 900	0	–26 700	–17 200	8 610
Orthoptera + Grylloblattaria + Phasmida + Dermaptera	–36 800	0	–	–	–	–	–18 400	18 400
Grylloblattaria + Dermaptera + Dictyoptera	–	–	–	–	–	–34 900	–34 900	–
Grylloblattaria + Zoraptera + Dictyoptera	–	–	–	–47 800	–58 300	–	–53 000	5 270
Mecoptera + Halteria	–67 800	–41 300	–	–	–	–	–54 500	13 300
Mecopteroidea	–393 000	–38 500	33 300	680	0	3 510	–65 700	66 200
Diptera + Mecoptera	–	–	–	–	–	–67 600	–67 600	–
Mecoptera + Diptera + Siphonaptera	–	–	–54 700	–160 000	0	–	–71 663	47 000
Zoraptera + Paraneoptera	–	–	–	–	–	–136 000	–136 000	–
Neuropteroidea + Mecopteroidea	–	–	–	–438 000	–11 200	–	–225 000	21 400
Halteria + Siphonaptera + Mecoptera	–406 000	–2350 000	–	–	–	–	–1380 000	970 000

Values rounded to three significant figures after calculation using values in Table 1. Phylogenetic relationships (Fig. 1) according to Wheeler *et al.* (2001), Kristensen (1995), Boudreaux (1979) or Hennig (1969). Ancestral state estimation by squared-change parsimony (sq-ch), and linear parsimony (linear) where possible. Clades are in order of the mean influence.

questions as it has answered. Future improvements may be expected both in general techniques and in the accuracy of the specific results presented here; for that reason this study should be viewed as preliminary. I detail some possibilities below.

In this study I have reconstructed realized diversification rates on internal branches as opposed to underlying tendency. Many realized shifts will not, because of the stochastic nature of speciation and extinction, represent shifts in underlying tendency. However, there are currently no methods which can estimate underlying tendency on internal branches for phylogenies like those used here. This is a worry, because existing optimal methods can probably never be used in many cases due to lack of phylogenetic information, whilst this study casts considerable doubt on the validity of methods that only consider a small number of higher taxa. The obvious solution is to develop a new method. The likelihood method developed by Sanderson & Donoghue (1994) for three-clade phylogenies is complex but could logically be applied to larger numbers of clades. In outline, the method first calculates the likelihood of a maximally complex model, in which every branch has a separate tendency to diversify. The likelihood of alternative simpler models is then compared with this. The simplest model with a likelihood not significantly different from the most complex is the one adopted. Whilst reasonably tractable in a three-clade scenario where the number of models is limited, for increasing numbers of clades the number of possible alternative models increases considerably. Implementing such a method would take some considerable development, but is not impossible given that similar difficulties have already been overcome, for example in the estimation of phylogeny. In the absence of such a method, however, the techniques outlined here provide a measure of compensation.

In many current macroevolutionary analyses, the assumptions about the radiation process are very simple (e.g. exponential clade growth, no extinction). This use of simple models is conservative, and perhaps reflects most our lack of knowledge of how clades do generally radiate. This study has not attempted to break the current mould in this respect. However, it seems likely that clades that genuinely do differ in one or more macroevolutionary parameters (e.g. rate of speciation) do not currently show up as different because of compensation by other parameters (e.g. carrying capacity of species, extinction rate). Distinguishing these differences is desirable. How we can make the step to parameter-rich models is presently unclear, for it would require a detailed knowledge of macroevolution, which conservative parameter-poor models are unlikely to provide. Methods incorporating different assumptions, if they could be justified, may give different results.

Despite increased use of phylogenetic information in this study relative to previous studies, the tips still represent higher taxa so if further radiations are nested within them, as seems likely, shifts in radiation rates across nodes are probably still overestimated throughout. The only way around this problem would be to have perfect knowledge of internal phylogeny (i.e. a species-level phylogeny), which for species-rich taxa is likely never to be achieved. However, any less inclusive taxonomic level, such as families, as the basis for the analysis would be an improvement. Limited phylogenetic information in many orders currently prevents that, although it is an achievable prospect.

This study, in common with most comparative studies, has used data only on extant taxa to draw inferences about past events. Extinct lineages, as well as one newly discovered order, the Mantophasmatodea, have been excluded because of lack of data, particularly about their phylogenetic relations. In addition the meaning of single-parameter constant rate models is unclear for taxa that were once diverse but are now extinct. Yet this has possibly introduced bias into the results, since extinct taxa possibly had lower intrinsic rates of cladogenesis than their extant relatives, and hence ancestors with lower diversification rates. The extinct hexapod orders belong mostly to the Palaeoptera and Polyneoptera (Carpenter & Burnham, 1985). Thus it is likely that the estimated realized diversification rates across nodes in these taxa are most affected. The proper way to incorporate information from extinct groups is in a comprehensive analysis of the fossil record (e.g. Labandeira & Sepkoski, 1993). Note also that if the phylogeny can be developed sufficiently, extinct taxa may not actually add much new information (see Nee *et al.*, 1994).

Another likely problem is that biases may have affected the estimates of taxon age. Here the approach taken was to minimize assumptions by using raw fossil data as far as possible. Phylogenetic assumptions, however, enforced some assumptions about missing fossil data, such that sister taxa are the same age. When the fossil record for a group is poor (such as for the Lepidoptera or Protura), the age assigned to it is likely to be more conservative for more derived taxa because fewer constraints are imposed by the fossil records of other taxa. The estimated age of Lepidoptera is consequently only constrained by the fossil record of two taxa (its own and that of the Trichoptera), whilst the ages of the primitive orders are constrained by the fossil record of every other hexapod order. This is a possible source of bias, although it can only be overcome by incorporating more detailed assumptions about the fossil record or further data, for example from molecular phylogenies.

Finally, methods for estimating ancestral states of continuous characters were employed here. Recent work (e.g. Webster & Purvis, 2002) has shown that these can prove unreliable, particularly if the character in question displays a temporal trend. A temporal trend in this context might include a tendency either for an increase or a decrease in diversification rate over time. The insect fossil record (Labandeira & Sepkoski, 1993) suggests that such trends probably do exist at least in some lineages, but they may be episodic and vary in direction. The effect of such changes on the validity of this analysis remains unknown.

CONCLUSIONS

At present, we cannot confirm the identity of the most influential shift in hexapod diversification. We can, however, conclude that one or more radiations within the Coleoptera have together been extremely influential, that the origin of Insecta was not, and that considerable attention should in future centre on the origins of the Neoptera, Holometabola, Pterygota and Eumetabola, all of which remain plausible candidates for, but none of which can be identified with certainty as, important shifts. Improvements in phylogenetic and fossil information and the development of methodology (particularly maximum likelihood techniques) for estimating rates on the internal branches of large but incomplete phylogenies are likely to help.

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