
Testing whether ecological factors promote cladogenesis in a group of tiger beetles (Coleoptera: Cicindelidae)

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We investigate the role of ecological differentiation in cladogenesis of a monophyletic group of North American tiger beetles, the subgenus *Ellipsoptera* (genus: *Cicindela*), by reconstructing their species-level phylogeny from mitochondrial DNA sequences. Observed reconstructions of ecological characters on the phylogeny are compared to those expected under simple null models of no association with cladogenesis. We find no evidence that ecological disparity is associated with either species coexistence, speciation or long-term persistence and/or radiation of lineages. Ecomorphological traits have evolved in response to differences in habitat occupied by species, but without detectable relationship with cladogenesis.

Keywords: species richness; cladogenesis; ecological diversity; DNA phylogeny; tiger beetles

1. INTRODUCTION

The splitting of single species into separate daughter lineages is a fundamental event in the evolution of clades, yet the causes of speciation and the proliferation of lineages remain unclear (Cracraft 1985; Maynard Smith & Szathmary 1995). Lineages may simply be separated by geographic division in parts of their ancestor's range, but an alternative is that ecological differentiation is a necessary component of the build up of species within clades (Richman & Price 1992; Van Valkenburgh 1995; Losos *et al.* 1998). Ecological differentiation may be important in promoting the early stages of speciation (Schluter 1996; Orr & Smith 1998) or play a role in the long-term persistence and subsequent radiation of lineages (Simpson 1953; Erwin 1992). There has been much debate on these issues, but the historical time-scale of the processes involved has meant that empirical evidence is scarce.

One recent approach for testing such ideas is to examine geographical and ecological patterns within closely related groups of species, in relation to their phylogeny. A phylogeny represents the pattern of cladogenetic splits leading to present-day species, so may reveal the processes operating during the radiation of clades. Factors involved in the separation of lineages are expected to display high variability between closely related species, for example habitat shifts within a radiation of Hawaiian spiders (genus *Tetragnatha*; Roderick & Gillespie 1998). In contrast, factors associated with long-term persistence and radiation are expected to show greater diversity among distantly related lineages, one possible example being nesting habit and life history in birds (Owens &

Bennett 1995). Furthermore, if ecological differentiation plays a role in species coexistence, we predict that co-existing lineages should display greater ecological differences than those found in different areas (Fjeldsa 1983; Butler & Losos 1997).

An important caveat to these predictions is that we may sometimes observe the predicted trends simply by chance, even if characters evolve at random and have no particular association with cladogenesis or coexistence (Cracraft 1990). Hence, we need to test whether the observed patterns are significantly different from those expected under null models of random accumulation of ecological disparity. We have introduced this approach elsewhere for analysing the geographical pattern of speciation (Barraclough *et al.* 1998; Barraclough & Vogler 1999) and develop it further in the current study.

To date, the approach has been limited by a scarcity of suitable phylogenetic data sets, particularly those including all species in a monophyletic group. In this paper, we analyse the diversification of a group of tiger beetles from the genus *Cicindela* based on their molecular phylogeny. *Cicindela* is one of the most diverse genera of insects, with approximately 1000 species worldwide, found in mainly dry or open habitats where they are active predators on arthropod prey (Pearson 1988; Pearson & Juliano 1993). Most species are narrow in their habitat choice, due to the requirements of both adults and larvae (Ganeshaiah & Belavadi 1986; Knisley 1987). The genus includes many well-defined species groups, representing ideal taxa for studying the build up of extant species from a single common ancestor (Vogler & Goldstein 1997; Vogler *et al.* 1998).

The subgenus *Ellipsoptera* is one such group, comprising 13 species, all of which are included in the current analysis. They occupy a range of habitat types in central and south-eastern USA (Pearson *et al.* 1997) and, thus,

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following the approach outlined above, we test whether habitat differentiation may have played a role in the splitting of lineages within this group. In addition, we consider two morphological characters with important functional consequences, body size and mandible length. Body size influences many aspects of an organism's biology, including energy budget (Pearson & Stemberger 1980), thermal properties (Pearson & Lederhouse 1987) and life history, whereas mandible length has been shown to determine the size of prey taken by *Cicindela* species (Pearson & Mury 1979; Ganeshaiyah & Belavadi 1986; Pearson & Juliano 1993). We investigate the relative roles of the external environment and species interactions on the origin of diversity in these traits and test whether morphological divergence may also be associated with cladogenesis in this group. Our aim is to identify patterns in the radiation of *Ellipsoptera* species, allowing future comparison with other groups to identify general 'rules' in the origin of taxonomic and ecological diversity.

2. METHODS

(a) *Phylogeny reconstruction*

We reconstruct the phylogeny of *Ellipsoptera* using DNA sequences. All experimental procedures followed those described in Vogler & Welsh (1997). In brief, DNA was extracted using a standard phenol–chloroform procedure, followed by PCR amplification and sequencing of three regions of the mitochondrial genome: cytochrome oxidase III (COIII, 634 base pairs (bp)), cytochrome *b* (CytB, 411 bp) and 16S rRNA (850 bp), a total of 1895 bp. Amplification of the CytB region resulted in multiple bands for several of the taxa. New primers were designed interior to the usual CBI–CB2 primers (Crozier & Crozier 1992) based on the known sequence for *Ellipsoptera hamata*. These primers amplified all *Ellipsoptera* and produced sequences similar in extent to those using the CBI–CB2 primers. We obtained sequences for all 13 *Ellipsoptera* species, plus three outgroups from other subgenera within *Cicindela* (*Cylindera debilis*, *Dromochorus belfragei* and *Cylindera celeripes*) shown to be close relatives by previous analyses (Vogler & Welsh 1997). A list of taxa and their collection records is provided at our Web site (<http://www.bio.ic.ac.uk/research/tigerb/>). Sequences have been submitted to GenBank (accession numbers AF132988–AF133035).

Data from all three regions were combined and analysed together. Shortest trees were determined using PAUP (Swofford 1993) with branch-and-bound search. Confidence in each node was assessed by determining Bremer support (Bremer 1994), namely the minimum length of trees constrained not to include the focal node. Constraints files for the tree searches were generated with TreeRot (Sorenson 1996). From the shortest tree, we calculated relative node ages for subsequent analyses by averaging reconstructed branch lengths between sister clades, starting from the tips and working towards the root. These estimates were directly proportional to those fitted using maximum likelihood assuming a molecular clock.

(b) *Geographical and ecological data*

Geographical ranges and habitat affinities were taken from Pearson *et al.* (1997) and a compilation based on literature and collection records and references therein. Body length and mandible length were measured from samples of individuals in the Natural History Museum collection. The data are available

on our Web site (<http://www.bio.ic.ac.uk/research/tigerb/>). We reconstruct the changes in each variable on the phylogeny using standard methods. Descriptions of habitats revealed four basic types: coastal salt marsh, sand dunes away from water, sandy river edges and salt flats and seeps in arid areas. Hence, we code habitat as a discrete, unordered, four-state character. Species in the latter two habitats apparently coexist in some localities, so we repeated the analyses lumping these into a single category: similar results were obtained. Changes were reconstructed onto the tree using parsimony. We performed all our analyses successively under both ACCTRAN and DELTRAN reconstruction algorithms, which represent extreme possible values of where changes occurred, with respect to our hypotheses. Our results are not qualitatively sensitive to these alternatives, so for brevity we present the results using ACCTRAN.

Body length, mandible length and latitudinal midpoint of species range were treated as continuous characters and changes reconstructed using independent contrasts. The change in morphology across a node was found to be proportional to molecular branch lengths, so we use standardized contrasts to represent the rate of change in each variable across each node (Felsenstein 1985). Mandible length correlates with body length (linear regression of contrasts $p < 0.001$), so we repeat subsequent analyses using both the residuals of mandible length from body length and absolute mandible length contrasts. The latter provides a more direct measure of prey size consumed by each species (Pearson & Mury 1979). Sample sizes of individuals in the museum collection were low for a few species, meaning species values may contain considerable error in those cases. To consider this possibility, we repeat all analyses recoding body length and mandible length as discrete characters based on significant differences among species and reconstruct the location of changes by parsimony, as described for habitat type. For each character, species were allocated into three groups (small, medium and large) on the basis of p -values from an analysis of variance among species.

(c) *Randomization tests*

We use randomizations to compare the observed patterns of ecological characters to those expected under null models of no association with cladogenesis and/or species coexistence. Our null model is that changes in each character occur at random and independently across the tree. If ecological change is associated with speciation, we expect that recently split species should display greater divergence than expected under the null model, given their short separation times and overall rates of change across the tree. In contrast, if ecological differences promote persistence and/or subsequent radiation, we expect greater divergence between more distantly related lineages. Hence, we test for a significant concentration of changes towards either the tips or the root of the tree. The null models are implemented by randomly shuffling observed changes among branches of the tree and recording where changes occur on the tree in each null trial (details in the legends for figure 1 and table 1). The two-tailed probability of the observed value is calculated from the expected distribution obtained by repeated randomizations. The tests are similar to those presented by Maddison (1990) and Butler & Losos (1997). We repeated our analyses for habitat type, body length and mandible length in turn.

We use similar tests to investigate the relative roles of the environment and species interactions in promoting ecological diversity. We consider the role of the environment by testing whether changes in the ecomorphological traits tend to occur in concert with changes in two measures of environmental

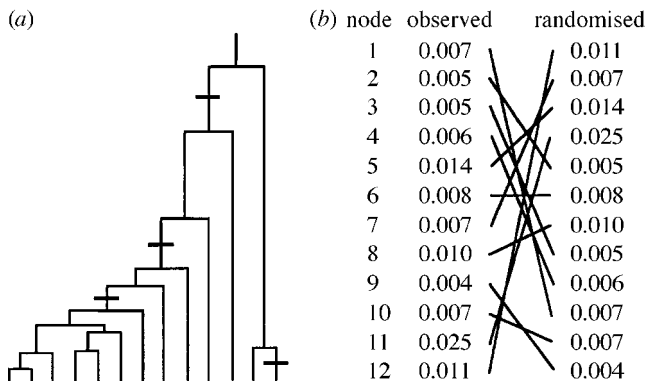


Figure 1. To test for significant departures from the null model that changes in each character occur at random across the tree and independently of one another, we randomize changes across branches on the tree. (a) For discrete characters, in each randomization changes are added at random to branches on the tree until the total number of changes reconstructed by parsimony equals the observed number (four in the above example). We treat the probability of change on a branch as proportional to its length (signifying a constant probability of change per lineage per unit time). (b) For continuous characters, observed changes are reconstructed as independent contrasts, representing rates of change occurring across each node. Randomization then proceeds by shuffling contrasts among nodes as shown. Tests were programmed in Microsoft Excel using Visual Basic.

variation, habitat type and latitude. Our null model is that changes in two variables, say body length and habitat type, evolve at random and independently. Hence, we randomly shuffle changes in each character across the tree and compared the observed association between pairs of characters to the distribution expected under randomization (details in the legend for table 1).

We investigate the role of species interactions by testing whether changes in ecological traits tend to occur between coexisting lineages, considering coexistence at two spatial scales. First, we test whether ecological changes coincide with high regional sympatry between lineages. Regional sympatry between sister clades at each node is calculated as

degree of sympatry

$$= 0.5 \times \left(\frac{\text{area of overlap}}{\text{range size of clade 1}} + \frac{\text{area of overlap}}{\text{range size of clade 2}} \right)$$

We then randomize changes in habitat type, body length and mandible length among nodes, holding sympatries fixed and test whether the observed association between ecological changes and sympatry differ from that expected under the null model. Second, on a finer scale, we test whether ecological differences evolve between locally co-occurring species. Co-occurrence is a property of pairs of species and so we use a modified test which considers whether pairwise ecological differences are associated with co-occurrence between species (co-occurring = 1 and non-co-occurring = 0; details in the legend for table 2).

3. RESULTS

The shortest tree is 669 steps in length (consistency index (CI) = 0.67 and retention index (RI) = 0.63) and provides strong support for relationships within the *Ellipsoptera* (figure 2). Note that relationships within the

Table 1. The pattern of ecological changes across the tree

(The pattern of variability in each character with respect to relative node age is expressed as the sum over all nodes of the amount of change occurring across each node X_i multiplied by the relative age of that node A_i $\sum_{i=1}^m X_i A_i$. For each test, the significance of the observed values was calculated from the null distributions obtained by 1000 randomizations (figure 1). Positive signs of association suggest that changes are concentrated towards the root and negative signs suggest changes occur near the tips. The associations between morphological changes and the environmental variables are expressed as the sum across all branches of the change in variable X , multiplied by the change in variable Y , $\sum_{i=1}^n X_i Y_i$. Positive signs suggest that changes in each character occur on the same branches and negative signs suggest that changes tend to occur on different branches. The associations between ecological changes and regional sympatry are expressed as the sum across all nodes of the change in variable X multiplied by the degree of sympatry S_i at each node, $\sum_{i=1}^m X_i S_i$. Positive signs suggest that changes in each character occur between sympatric sister clades. Results are shown for both continuous and discrete formulations of the morphological variables. Results are shown for absolute mandible length; patterns for mandible length relative to body length are discussed in the text.)

	discrete		continuous	
	sign	p	sign	p
habitat \times node age	+	0.61	—	—
body length \times node age	—	0.16	—	0.22
mandible length \times node age	+	0.20	—	0.35
body length \times habitat	+	0.73	+	0.78
mandible length \times habitat	+	0.02	+	0.32
body length \times latitude	—	0.40	+	0.19
mandible length \times latitude	—	0.40	+	0.84
habitat \times sympatry	+	0.59	—	—
body length \times sympatry	—	0.99	—	0.49
mandible length \times sympatry	+	0.39	—	0.25

crown group differ from those found in a preliminary tree presented elsewhere (Barraclough *et al.* 1998) due to the inclusion of additional sequences using the newly designed CytB primers. In addition, contrary to a previous morphological phylogeny of *Ellipsoptera* (Willis 1971), our data provide no evidence for monophyly of the three sand dune species, *Ellipsoptera hirtilabris*, *Ellipsoptera gratiosa* and *Ellipsoptera lepida*: forcing them into a monophyletic group leads to a tree that is significantly longer than the shortest tree (Kishino–Hasegawa test, $p < 0.05$).

The reconstructions of changes in each variable are shown in figure 3 and the results of randomization tests in tables 1 and 2. We find little evidence for the role of ecological factors in cladogenesis. None of the characters displays a significant concentration of changes towards either the tips or the roots of the tree. Changes in habitat affinity are found predominantly among older nodes, but those nodes are separated by longer branches, as expected for exponentially growing clades and the observed concentration is not significant under the null model that the probability of change is proportional to branch length. Body length and mandible length display greater variability among recent nodes than habitat type, but morphological differentiation between recently split species is not

Table 2. *The pattern of pairwise ecological differences between species*

(The pattern of variability in each character is expressed as a pairwise matrix of ecological differences between all species pairs.

	2	3	<i>n</i>
1	$X_{1,2}$	$X_{1,3}$	$X_{1,n}$
2		$X_{2,3}$	$X_{2,n}$
3			$X_{3,n}$
·			..	·
<i>n</i> - 1				$X_{n-1,n}$

Pairwise differences take values of 0 (same) or 1 (different) for discrete characters or the absolute difference in species values for continuous characters. The association between ecological differences and local co-occurrence is then expressed as the sum across all species combinations of the product of the pairwise ecological difference ($X_{i,j}$) and the co-occurrence of each species pair ($C_{i,j}$), $\sum_{i=1, j=i+1}^{i=n, j=n} X_{i,j} C_{i,j}$. Positive signs of association suggest that co-occurring species tend to display the greatest ecological differences and negative signs suggest similarity of co-occurring species. Although this measure is based on pairwise distances, the significance of the observed value is calculated, as before, by randomization of changes among nodes in the tree, so the test incorporates non-independence among pairwise comparisons expected due to phylogeny. The distribution of pairwise differences fluctuates widely among randomizations and so, to reduce this effect, we scale each pairwise difference ($X_{i,j}$) by the mean of the pairwise differences obtained for that character ($\sum X_{i,j}/n$) in each randomization. The test is repeated for regional sympatry. This test was designed to retain information on which species combinations are sympatric or co-occurring, rather than averaging sympatry at a node as in table 1, providing a potentially more sensitive test for the role of species interactions.)

	discrete		continuous	
	sign	<i>p</i>	sign	<i>p</i>
habitat × sympatry	+	0.78	—	—
body length × sympatry	+	0.38	+	0.68
mandible length × sympatry	+	0.34	—	0.33
body length × co-occurrence	—	0.49	—	0.50
mandible length × co-occurrence	—	0.79	—	0.10

significantly greater than expected under the null model. As described elsewhere, the pattern of sympatry between sister clades suggests that changes to species ranges have occurred in the *Ellipsoptera*, such that current ranges may provide little record of ranges at speciation (Barraclough *et al.* 1999; Barraclough & Vogler 1999).

In addition, we find no evidence for the role of species interactions in promoting ecological divergence, but instead that differences among species appear to reflect the environment occupied by those species. From the reconstructions in figure 3, both body length and mandible length appear to be associated with the habitat occupied by each species, with the three sand dune species significantly smaller than all other species. Randomizations suggested the pattern relates most strongly to mandible length, revealing a significant association under discrete coding. No relationship was found using the residuals of mandible length from body length, suggesting

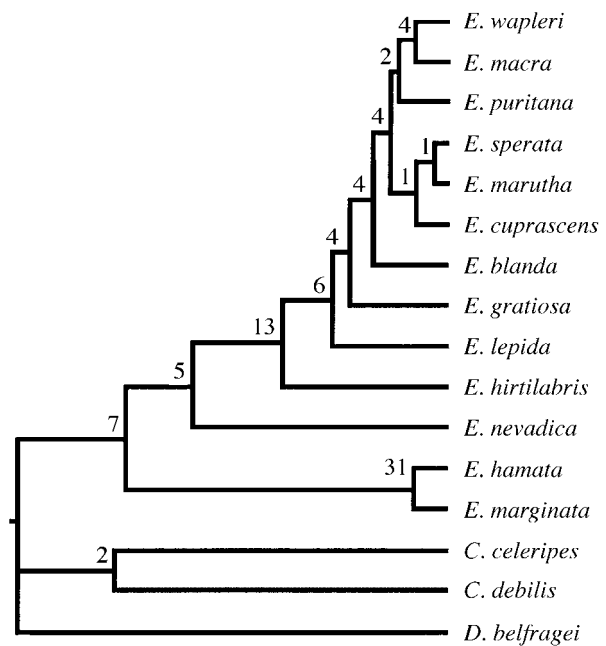


Figure 2. Single most parsimonious tree of the *Ellipsoptera* based on combined mitochondrial DNA sequence (total length = 669 steps, CI = 0.67 and RI = 0.63). Bremer support values for each node are shown, representing the increase in tree length at which each node is no longer resolved. The search methodology is described in the text. The three genes (16S, CytB and COIII) provide consistent support for the shortest tree, but with a weaker signal when each is analysed separately. All searches and support measures were calculated without constraining to a molecular clock, but we show the branch lengths used in subsequent analyses, calculated by applying a local molecular clock procedure to the shortest tree (details in §2).

that, if real, the pattern relates to absolute mandible length rather than relative mandible length or body length. No significant relationship is observed under continuous coding, the difference apparently arising because independent contrasts consider overall change across a node, rather than which branches changes occur on. If we include the signs as well as magnitudes of changes at a node in the continuous test, we obtain a significant association between mandible length (but not body length) and habitat differences ($p < 0.05$, randomization test). There is no relationship between latitude and morphology.

We find no evidence for character divergence of body length or mandible length between sympatric or co-occurring species or for habitat segregation between regionally sympatric species in any of our tests (tables 1 and 2). Ecological divergence is unrelated to the regional sympatry between sister clades (figure 3 and table 1) and locally co-occurring species tend to display, if anything, greater morphological similarity than expected under the null model, although the trend is not significant (table 1).

4. DISCUSSION

Our analyses use phylogenetic reconstructions to investigate the role of ecological differentiation in cladogenesis and species coexistence of a monophyletic group of tiger

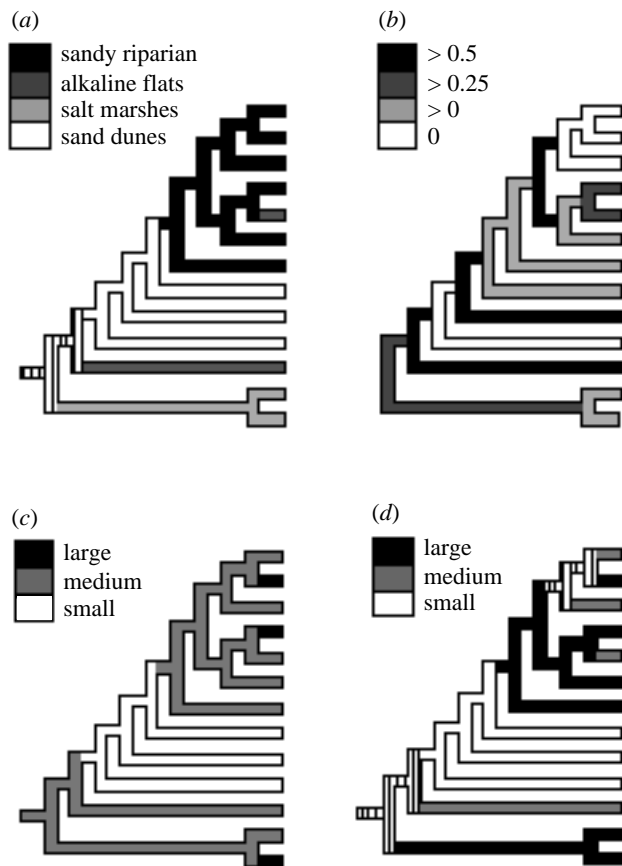


Figure 3. Reconstructions of character changes onto the tree using MacClade (Maddison & Maddison 1992), showing the consensus of all most-parsimonious solutions. Taxon names are shown in figure 2. Details of character coding are provided in §2. Note that sympatry is also shown, not as a standard character, but with colour coding representing the present-day degree of regional sympatry between sister clades at each node. (a) Habitat type, (b) sympatry, (c) body length and (d) mandible length.

beetles, subgenus *Ellipsoptera*. To assess the significance of observed patterns, we use randomization tests to compare reconstructions of character changes with those expected under simple null models of no association. We find no evidence for greater ecological differentiation between recently split species than expected if ecology evolves independently of speciation events. Similarly, we find no evidence that differentiation between basal clades is greater than expected if differences in ecology accumulate at random over time; hence, there appears to be no influence on persistence or subsequent radiation of those lineages. Ecomorphology appears to evolve in concert with changes in the habitat occupied by species, suggesting that the environment determines ecomorphology rather than species interactions. We find no evidence for divergence of morphology between coexisting species, at either regional or local spatial scales.

These results fail to support a role for species interactions in promoting diversity in the ecological traits studied. Field evidence suggests that local interactions do occur among species of tiger beetles (Pearson & Knisely 1985) and that our chosen characters, particularly mandible size, do have a direct influence on resource use (Ganeshiah & Belavadi 1986; Pearson & Juliano 1993),

but we observe no divergence between coexisting species. One possible explanation is that the effects of interactions among clade members may be obscured by interactions with other species groups of tiger beetles and future work will address this possibility. Alternatively, the strength of interactions may be weak compared to selection imposed by the physical environment. If communities represent transient groups of species, as suggested by the fossil record for many groups, particularly north temperate insects (Coope & Wilkins 1994; Elias 1994; Jablonski & Sepkoski 1996), then the strength and direction of species interactions may be highly variable over time. The pattern of geographical ranges in *Ellipsoptera* supports this possibility, with evidence for extensive range movements (Barraclough *et al.* 1999). Our results suggest that, while there may be interactions between *Ellipsoptera* species where they co-occur, interactions do not have long-term consequences for divergence at the species level. Instead, ecomorphological divergence, specifically in mandible length, relates to differences in habitat occupancy among species. This pattern is supported by field studies which demonstrate close fits between (i) habitat type and prey size distribution, and (ii) mandible length and size of prey available to tiger beetles (Pearson & Mury 1979; Ganeshiah & Belavadi 1986). It also reflects a large body of evidence for environmental correlates of ecomorphology, supporting a possible role for environmental constraints in structuring species assemblages (Wainwright & Reilly 1994; Losos *et al.* 1997; but see Dayan & Simberloff 1998).

In addition, our analyses provide no support for the role of ecological differentiation in cladogenesis of the *Ellipsoptera*. Most accounts of adaptive radiation propose that ecological differences reduce the strength of interactions among species, thereby enhancing the persistence, coexistence and radiation of lineages (Simpson 1953; Hutchinson 1959; Erwin 1992). The previous discussion suggests that this process does not apply for the characters we consider. However, even in the absence of interactions, ecological factors may still play a role in cladogenesis, for example if heterogeneity in the external environment promotes species divergence (Hodges & Arnold 1994; McMillan *et al.* 1997; Smith *et al.* 1997). Hence, we present a direct phylogenetic test for characters associated with speciation and persistence and/or radiation. Our approach is to test for a significant concentration of changes in ecological characters towards more recent or older nodes within the phylogeny, respectively, compared to the expected distribution of changes under a standard constant rate model of character evolution. No trait we consider shows any significant departure from the null model. Other methods may be applicable for estimating the amounts of change at speciation events (for example Martins & Hansen 1997; Pagel 1997; Schluter *et al.* 1997), but have not yet been applied to the specific questions we address. Future work is needed to assess the use of our approach and these possible alternatives.

In conclusion, we find no evidence that ecological disparity is associated with cladogenesis or species coexistence in *Ellipsoptera*. The classic examples of adaptive radiation, in which ecological differentiation is intimately linked to speciation and persistence of lineages, are found almost

exclusively on islands or island analogues (Schluter 1996; Roderick & Gillespie 1998; but see Cameron *et al.* 1996). Continental areas may represent more open systems, with greater freedom of movement of species ranges and greater fluctuations in species abundances (Irschick *et al.* 1997), leading to much weaker interactions within clades. Our study concerns a single, small clade of tiger beetles and more work is needed to assess the general applicability of the methods and findings we present. Phylogenetic analyses provide a critical framework for evaluating the importance of ecological disparity in cladogenesis across a range of groups and environments.

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As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.

