Mapping extrinsic traits such as extinction risks or modelled bioclimatic niches on phylogenies: does it make sense at all?

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Abstract

An increasing variety of extrinsic traits are used in comparative studies aimed at testing evolutionary hypotheses. After briefly reviewing the relevant literature, it appears that three different problems are implied by this trend. Some extrinsic traits are only surrogates for phenotypic traits, and should be redefined to better fit the requisites for phylogenetic analysis, such as selective regimes and extinction risks. Some others are already adequately defined and cannot be made less extrinsic, such as taxon age, geographical distribution, associates (parasites, symbionts, etc.), and bioclimatic modelled niches. Because they are not heritable, they should not be analysed by optimization onto a tree, but are better considered in sister-group comparisons or within a reconciliation procedure, as already done for areas of biogeography.

Phylogenetic approaches to extinction risk (Cardillo et al., 2005) have recently generated a controversy. Putland (2005) and Harcourt (2005) have justly remarked that a phylogenetic analysis of such an extrinsic trait does not make sense: the evolution of a trait that does not evolve cannot be reconstructed. This is not the only case of traits inappropriately analysed in a phylogenetic context, and we submit that there is a recurrent and misleading trend of analysing extrinsic, and therefore non-heritable, traits. We try to understand why this problem has occurred repeatedly, and how these studies could be carried out in a more appropriate way.

Many evolutionary studies consider trait changes on previously reconstructed phylogenetic trees (Brooks and McLennan, 1991; Eggleton and Vane-Wright, 1994; Grandcolas et al., 1994). Because these traits of interest are most often defined in ecological or evolutionary studies, independently of any phylogenetic analysis, they do not necessarily fit the basic requirements for phylogenetic characters. They can be too vaguely defined, and may merely represent general classes rather than accurate descriptions of organisms. For example, this is often the case for broad categories used for ecological or behavioural classifications, but which do not describe properly the details of the behaviours of different species, as criticized by many authors (Mickevich and Weller, 1990; Wenzel, 1992; Deleporte, 1993; Grandcolas et al., 1994, 2001; Proctor, 1996; Luckow and Bruneau, 1997). A vague definition is, however, not such a big problem. More specific studies can simply be carried out to document the details of the trait occurrences in different taxa. Sometimes these details are already known and just need to be taken into account, with an appropriate methodology, to build the phylogenetic analysis of trait evolution (e.g. Coddington et al., 1997; Desutter-Grandcolas and Robillard, 2003; Grandcolas and D'Haese, 2004).

A more serious problem occurs when the traits of interest are defined in such a way that they are not really "heritable" sensu lato (not referring specifically to the statistical heritability in population genetics); or, more generally, when the traits are defined as extrinsic to the taxa, as criticized by Grandcolas et al. (2001) and Grandcolas and D'Haese (2003). There are many

different cases of this kind in the literature, and their comparison is informative. Among such extrinsic traits, we will survey first, those that appear not to be phenotypic, and therefore deserve to be analysed with a procedure other than optimization on the tree; and second, those that appear to be questionable surrogates for phenotypic traits.

We found four kinds of extrinsic trait that are non-phenotypic: taxon age, geographical distribution, associates (parasites, symbionts, etc.), and bioclimatic modelled niches.

The first—taxon age—involves stratocladistics, which includes ages and stratigraphic distributions of taxa in the phylogenetic analysis (Vermeij, 1999), a practice that has been criticized (e.g. Geiger et al., 2001), but is still regarded as valuable (Fisher, 2008). Fisher (2008, p. 376) recognizes that the age of a taxon is not heritable, but he maintains that it can be used as a character because, in his own words, ''The apple falls not far from the tree''—age not descending with modification *per se*, but modifying continuously. Fisher also accepts that age cannot be interpreted in terms of homology, but again holds that ''temporal order carries information'' (ibid.). These statements show that stratigraphic ages do not fit requirements for phylogenetic analysis of evolutionary changes, even if they have sometimes been analysed that way for operational reasons. On one hand, stratocladistics makes the assumption that temporal order provides operational information complementing the actual evolutionary information residing within the phenotypic traits of the organisms. On the other hand, this information is irrelevant for establishing phylogenetic relationships, as ages carry no homology information, so that we could change the saying for a deceptive ''apples fall not far from many different trees.'' Therefore taxon age cannot be a phylogenetic character.

Distributional data have sometimes been considered as better studied if included in the phylogenetic analysis (Zrzavý, 1997), a practice difficult to accept, given that areas do not evolve as phenotypic traits and are not heritable (Nelson and Platnick, 1981; Kluge, 1989; Grandcolas et al., 2001). As clearly summarized by Hovenkamp (1997), areas evolve by themselves and are not expected to differentiate strictly by divergence.

In another line of reasoning, Freudenstein et al. (2003) have argued that among extrinsic traits, some are indispensable to organisms, such as gut symbionts of termites; and some are not, such as specific habitats from which species could be extirpated and still survive (their own examples). According to this rationale, the former traits should be considered in a phylogenetic analysis, while the latter ones should not. This is a strange way to discriminate among extrinsic traits in evolutionary studies because it does not rely on any descent criterion, and rather makes a very risky evolutionary guess about the significance of indispensability. Termite symbionts can evolve on their own despite their tight association with termites (some termites have lost their symbionts; Legendre et al., 2008), while specific habitats are directly related to species preferenda (behavioural or physiological responses to the environment), which are phenotypic heritable traits. Phylogenies of symbionts can be inferred and compared with host phylogenies. Habitats and preferenda are simply in need of careful definition.

Finally, the so-called modelled bioclimatic niches are often optimized on phylogenetic trees to assess the evolution of species preferenda (e.g. Graham et al., 2004; Martínez-Meyer et al., 2004; Yesson and Cullam, 2006). Theoretically, the ecological niche (the way the environment is used) is an intrinsic property of the species and is very close to phenotypic traits (the behavioural or physiological responses to the environment). However, practically, the so-called modelled bioclimatic ''niches'' are merely climatic domains corresponding to the locations where one species has been found (Soberón and Peterson, 2005; Peterson, 2006). These domains depend directly on the distributional areas of species, and their definition can be biased by geographical sampling problems (e.g. the truncated response curve, different factors operating at different spatial scales: Austin & Gaywood, 1994; Mackey & Lindenmayer, 2001). Despite the appealing reference to the phenotype in the term ''niche'', and because of the way they are defined, these bioclimatic domains are not plainly heritable and intrinsic features of species. To our knowledge, no-one has yet objected to the phylogenetic analysis of bioclimatic modelled niches, but some more reasonable approaches have been proposed without assuming that bioclimatic domains evolve as phenotypic traits. Bioclimatic modelled niches can be compared among sister-groups (Knouft et al., 2006; Murienne et al., 2009) or used as an ecological control for historical biogeographical inferences (Carstens and Richards, 2007), instead of being optimized on the tree, which would mean that bioclimatic domains are inherited as such by descent with modification. Certainly, niches can be studied differently at a more accurate scale, and heritable behavioural responses can be described that could be optimized on a tree. But this is another matter that the so-called modelled niches based on species distributions.

We now deal with extrinsic traits identified as surrogates for phenotypic traits. Classically, a phylogenetic and comparative study involves sampling character states in every taxon concerned. This is a hard job, especially for traits that cannot be sampled from collection specimens (unlike morphology or DNA), or from their record of, for example, distribution and its ecological correlates. Therefore many studies take a short-cut by replacing observations on the phenotype with some more available proxies. Then, the surrogate is

not only a broad and poorly defined substitute for a phenotypic trait, but rather a different trait, definitely extrinsic.

This is the case of the analysis of adaptation based on the phylogenetic patterns of both the trait and its selective regime (Baum and Larson, 1991). Generally, selective regime—"all such environmental and organismic factors that combine to determine how natural selection will act" (Baum and Larson, 1991, p. 2)—is not studied, but assumed according to a function associated with the trait of interest and used as a surrogate for selective pressure (e.g. function "way of life, terrestrial versus scansorial" and trait "leg morphology" in salamanders; Baum and Larson, 1991). Grandcolas and D'Haese (2003) and Grandcolas (2009) criticized this approach, arguing that selective pressure is not heritable and that trait functions are misleading surrogates for natural selection. Yet this adaptationist protocol is still widely used (e.g. Scales et al., 2009). Adaptation would be better studied by a combination of phylogenetic and population approaches, focusing, respectively, on the phylogenetic patterns of the trait and its function, and their selective value in various populations (Carpenter, 1989; Grandcolas et al., 2001; Grandcolas and D'Haese, 2003).

As already mentioned, surrogates for extinction risks have been mapped on phylogenetic trees to detect any correlation with taxonomic belonging or history (Fisher and Owens, 2004; Cardillo et al., 2005). Putland (2005) criticized this approach, remarking that extinction risk is not a phenotypic trait; Harcourt (2005) argued that these studies poorly assessed extinction risks by using International Union for Conservation of Nature and Natural Resources (IUCN) Red Lists as surrogates. Purvis (2008, p. 310) maintained that the approach makes sense for detecting both taxonomic biases and extinction proneness. He emphasized on the so-called phylogenetic confusing effect in taxonomic comparisons. The real problem is that there is no way to know which kind of bias will be introduced if an extrinsic surrogate (extinction risk instead of body size, life histories, etc.) is used in a phylogenetic perspective, and the results are simply not interpretable. The question therefore is not about biasing or neglecting possible phylogenetic effects concerning extinction risks (Purvis, 2008), but about studying those risks by considering the appropriate phenotypic heritable traits in a phylogenetic perspective.

This rapid overview of the literature has shown that many different research fields have a tendency to use non-heritable and extrinsic traits in a phylogenetic context. These approaches are, however, not all the same, and they clearly imply three different kinds of problem.

As a first problem, comparative studies, like others, are sometimes done quickly at the cost of data quality. Some studies are based on a procedure where actual phenotypic traits are replaced by approximate surrogates already available in the literature. This is the most disputed approach as it is plagued not only by poor definition of the trait of interest, but also by a substitution, which can be misleading. This is the case for selective regimes or extinction risks. One could use proper words by replacing "selective regime" by "trait function" (definitely not a selective value); and, instead of Red Lists, use the phenotypic traits that are already known to influence extinction risks. There is no originality in using a fast and possibly misleading surrogate procedure for large-scale scientific studies, and the remedy is simply to encourage critical examination of any phylogenetic approach.

A second and more specific problem is implied by the "phylogenetic correction" (e.g. independent contrasts method, Felsenstein, 1985) mainly used in the framework of the so-called "comparative method" (Harvey and Pagel, 1991). This practice, consisting of extracting a phylogenetic effect (as nicely characterized by Coddington, 1994), was originally conceived in a pre-phylogenetic epoch to remove pseudoreplication biases in taxonomic comparisons (Clutton-Brock and Harvey, 1979). We are now able to build large and detailed trees on which ancestral changes in character states can be reconstructed within the nested subsets of taxa, and therefore pseudoreplication biases cannot be generated any more. In addition, these phylogenetic analyses of evolution do not obscure the precise pattern of trait evolution by hiding local correlations and associations or character-change polarities, as did the "phylogenetic correction". "Phylogenetic correction" must therefore be abandoned as an outdated perspective and we should turn toward phylogenetic analyses of trait of interest.

A third problem is that some traits can be especially relevant in some evolutionary studies, but too extrinsic to be mapped on phylogenies. They cannot be better defined and replaced by more intrinsic and actually phenotypic traits. Distributional areas, or their associated bioclimatic niches and strata of fossil taxa, deal with the physical environment and the spatial or temporal distribution of taxa, a property that the taxa conserve mainly through inertia (because of dispersal limitations or geographical constraints), and only partly because of their physiological responses to the environment. We submit that these traits should be better analysed within the careful framework defined by biogeography. In biogeographical approaches aimed at understanding the distribution of one clade (Hovenkamp, 1997), the phylogeny of the clade is compared with a tree of areas through a reconciliation procedure to identify vicariance, dispersal, and extinction events (Nelson and Platnick, 1981; Page, 1994; Charleston, 1998). Areas are therefore treated adequately as non-phenotypic traits that evolve on their own (mountains or

rivers can move; climates can change), the evolution of which can be compared with that of taxa. Associated taxa, such as symbionts or parasites, are in the same case with respect to their hosts and, actually, are already most often studied with the same reconciliation procedure.

In conclusion, the growing and beneficial involvement of phylogenetics in any branch of evolutionary biology will certainly cause recurrent interest in traits that are not orthodox phylogenetic characters. By distinguishing between surrogates to be defined more accurately, and truly extrinsic traits to be studied in a specific way, such evolutionary studies will have more opportunities to carry out adequate and powerful analyses.

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