

COMMENTARY ON LOSOS (2008): NICHE CONSERVATISM DÉJÀ VU

There is much debate in the recent literature over whether niches are generally conserved or not. I have argued that this debate is not very fruitful, because niches are presumably neither identical nor completely different between close relatives, and the answer simply depends on the scale and details of the test (Wiens & Graham 2005). Instead, a more useful focus may be on testing for the patterns that niche conservatism may (or may not) help create and explain. As one example, we reviewed how NC (niche conservatism) in climatic tolerances may limit the geographic ranges of species, and the myriad effects that this may cause (and patterns it may help explain). These include patterns of species richness, historical biogeography, community structure, allopatric speciation, spread of invasive species, and responses of species to global warming. We described how these effects can potentially be tested using ecological niche modelling and related approaches, especially when combined with phylogenies (our Table 1).

In a thought-provoking article, Losos (2008) argues that evidence for NC is equivocal, and that NC must be tested rather than assumed. I strongly agree that there is abundant evidence for niche lability and that NC should be tested rather than assumed *a priori*. But without attention to specific effects of NC, these tests risk being meaningless. This criticism may apply to many counter-examples to NC mentioned by Losos.

For example, Losos advocates testing NC based on the fit of an ecological trait to a Brownian motion model across a phylogeny (e.g. a GIS-based climatic variable; Knouft *et al.* 2006). But what exactly do we learn from this exercise? For example, does it tell us if there is a sufficient or insufficient level of NC to create patterns of speciation, species richness, community structure, spread of invasive species, or responses to global warming? Clearly, the answer is 'no'. Then what is it actually telling us? A useful test of NC requires a specific context.

In addition, this tree-fitting approach (by itself) may be fundamentally inadequate to address the diverse effects of NC described above, because it only considers where species occur. But it is essential to also consider where species are absent, given that their failure to occur there may be a consequence of NC. For example, allopatric sister species on adjacent mountain ranges may have somewhat different climatic niches. Yet, the primary factor that caused them to be allopatric (and thus, speciate) may be inhospitable climatic conditions in the intervening lowlands, where neither can persist because of NC (Wiens & Graham 2005; Kozak & Wiens 2006). The tree-fitting approach alone may

not reveal this pattern, because it ignores data from the localities where the species are absent.

As a sole approach to testing NC, the tree-fitting approach is blind to the different scales at which NC may be important. Just because a trait shows some variation across species within a clade does not mean that NC was not important in splitting a particular pair of species, limiting the spread of an invasive species, or driving large-scale patterns of historical biogeography and diversity in the group.

An example from Losos' outstanding work on *Anolis* lizards may illustrate both the problems of ignoring scale and of considering only where a clade or species occurs. Knouft *et al.* (2006) argued that climatic niches were not conserved among species of the *sagrei* group on the tropical island of Cuba. One species of the group (*A. sagrei*) has become invasive in Florida. Despite extensive spread in Florida over > 100 years, it has failed to invade more temperate regions of North America (Kolbe *et al.* 2004), a potential signature of NC.

At a larger scale, over the entire phylogenetic history of the genus, *Anolis* have generally failed to invade cool temperate and desert regions, such as northeastern and southwestern North America (Conant & Collins 1998). This pattern may also reflect NC. But this dramatic pattern is completely invisible if one only considers climatic data from where *Anolis* species occur. Thus, it seems problematic to analyze climatic variation within a group of exclusively tropical organisms and conclude that their climatic niches are not conserved. As suggested by *Anolis* lizards, some niche lability among species within a clade may not rule out effects of NC on other scales, such as limiting the spread of invasive species (short term) or determining large-scale patterns of biogeography and diversity (long term).

Losos' criterion for NC may underlie his argument that NC is not a process. If NC is simply considered the match of an ecological variable to a phylogeny, then there is no reason to think about it as a process that helps create other biological patterns. Losos argues that NC is not a process because many different processes may cause it. But many well-known processes are actually caused by a variety of different processes when viewed at a finer scale. For example, a variety of genetic mechanisms can lead to speciation (e.g. polyploidy, sexual selection). NC, like speciation, is a pattern and a process. But it can sometimes be useful to talk about both as processes, because they can create other patterns (e.g. NC may limit geographic ranges, speciation creates species and phylogenies).

I strongly agree with Losos that statistical tests of NC are needed, rather than uncritically assuming it to be universally present in every case. But those tests must be appropriate for the scope and scale of more specific questions, or else they risk being irrelevant. There is no

'one size fits all' test for NC, because the effects of NC may be manifested in different ways and at different scales. If we match our tests to specific questions and appropriate scales, then existing studies already suggest that considering NC can potentially help answer some fundamental questions in ecology, evolution, and conservation, such as why there are more species in the tropics (e.g. Wiens *et al.* 2006), what drives the origin of species (e.g. Kozak & Wiens 2006), and what determines the spread of invasive species (Peterson 2003).

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REJOINDER TO WIENS (2008): PHYLOGENETIC NICHE CONSERVATISM, ITS OCCURRENCE AND IMPORTANCE

Phylogenetic niche conservatism (PNC) – the tendency of closely related species to be similar in their niches – is the subject of considerable research in recent years. Because some workers appear to assume that PNC inevitably will occur, I pointed out that, in fact, in many cases clades do not exhibit PNC for some ecological traits (Losos 2008). Consequently, I cautioned that scientists conducting research in which the phylogenetic distribution of ecological traits might be relevant should directly test whether PNC occurs, rather than assuming that it does. In addition, I mentioned a number of the implications of lack of PNC for a wide variety of studies.

I agree with John Wiens about many of the issues he raises. In particular, we agree that PNC may be relevant to understanding many phenomena, such as how and why

speciation occurs and the biogeographic distribution of a clade. In his Comment, Wiens (2008) raises a number of objections to my paper, but I believe that they primarily represent misunderstanding of what I was trying to say.

Wiens read my paper as a call for researchers to go out and determine the extent of PNC for no other purpose than to see how prevalent it is. But this was not my intent at all. Quite the contrary, my purpose was to say that if a researcher is conducting a study in which the existence of PNC may be relevant to the study's design or interpretation, then the researcher should directly examine whether PNC occurs, rather than just assume that it does. Perhaps I should have said this more explicitly, but I thought the point was implicit in the discussion in the 'Implications' section and elsewhere in the paper.

Wiens also argues that context and scale are important in considering PNC. Reiterating Wiens & Graham (2005), he states, 'niches are presumably neither identical nor completely different between close relatives, and the answer simply