'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

depends on the scale and details of the test'. Wiens cites the example of a clade of Cuban *Anolis* lizards that exhibits no phylogenetic signal in climatic niche – closely related species are no more ecologically similar in climatic niche than are distantly related species (Knouft *et al.* 2006). Yet, at a higher level, PNC certainly exists, because the entire genus of *Anolis*, almost 400 species strong, is geographically restricted, primarily to tropical areas.

I agree with this perspective and noted in my paper that a trait that exhibits no PNC within a clade might nonetheless exhibit PNC at a higher phylogenetic level. But, given that PNC is scale-dependent, what are we to do with this information? To turn Wiens' example around, should we go from the observation that all *Anolis* exhibit a phylogenetically inherited constraint (selective or otherwise[1]) that prevents them from occupying cool temperate localities to the conclusion that among a subclade of *Anolis* found exclusively in the tropics, we would expect the most closely related species to be the most ecologically similar? Of course not; the observations are on different scales and not commensurate. Similarly, would it be reasonable to extrapolate from the lack of phylogenetic signal among a clade of tropical lizards to expect that members of that clade have inherited no factors limiting their evolutionary potential at all, and thus could adapt to any habitat, even those beyond the tropics, such as temperate habitats, or even polar climates? Again, this would be unreasonable. Rather, conclusions about PNC are applicable only to the clade under study and to the environmental conditions experienced by those clade members. Extrapolating beyond those conditions is unwarranted.

Suppose, then, we wanted to study why *Anolis* has a limited distribution. Anoles do not occur in cool temperate regions. How could the lack of use of such habitats be incorporated into a study of PNC? Because no anoles occur in cool temperate areas, a phylogenetic analysis limited to anoles would not be informative – it would only tell us whether phylogenetic effects occur over the range of habitats anoles occupy, but would be silent about those habitats not used by any species in the clade. This is the point Wiens makes.

The answer is to address the question at the appropriate phylogenetic scale. The question is: are anoles unable to use cool temperate habitats due to some phylogenetically inherited feature? To test this question, we would need to broaden the phylogenetic scope to include related taxa that do occur in such habitats; only at this scale could we investigate whether the failure of anoles to occupy those habitats is phylogenetically non-random. Among the lizard family Iguanidae, to which anoles belong, several clades include species living in climates not used by anoles, including cool temperate regions. A phylogenetic analysis of the Iguanidae probably would indicate strong PNC of climatic niche. From such an analysis, we could conclude that the anole clade has inherited some aspect of their biology that has limited their ability to invade cool temperate regions; we would further conclude that unless this constraint is broken, anoles will continue to be unable to invade in the future.

Wiens, comments are also relevant to an issue I have heard from others: just because PNC does not occur in a clade, how do we know that some subclade does not possess phylogenetically shared factors limiting their evolutionary potential? Of course, the answer is that we do not know this – just because an entire clade shows no statistical evidence of PNC does not mean that it does not occur within subclades. Again, this is a matter of scale, and the only way to investigate PNC for a particular subclade is to devise the appropriate test at the appropriate scale, just as Wiens prescribes.

In summary, I think John Wiens and I agree on most issues. In particular, we agree that in studies concerning the ecology of related species, PNC should be measured, rather than assumed, and that such studies should be conducted at the appropriate phylogenetic scale.

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[1]This illustrates why PNC is a pattern, not a process. The existence of PNC simply tells us that some closely related species share some attribute that limits their ability to adapt to certain conditions, and that they are thus more similar than might otherwise be expected. Many different processes could cause such evolutionary limitation, as discussed in my article and Wiens & Graham (2005). The existence of PNC indicates some process is at work, but does not inform as to what it is. Although referring to phenomena such as PNC may be a convenient shorthand expression, it risks confusing workers who may come to believe that phylogeny itself somehow acts mechanistically to constrain or direct evolutionary change.

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