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The Checkered History of Checkerboard Distributions: Reply

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Diamond et al. (2015) raise three criticisms of Connor et al. (2013). The first is that by analyzing each archipelago separately rather than analyzing species pairs using their entire or global geographic ranges, Connor et al. (2013) have misinterpreted the factors that affect the geographic ranges of congeneric species pairs. The second is that Connor et al. (2013) did not plot the geographic ranges of species pairs. Finally, Connor et al. (2013) did not include information on vagrancy.

The checkered history of checkerboard distributions is characterized by its pioneer (Diamond 1975) and subsequent followers (Diamond and Gilpin 1982, Gilpin and Diamond 1982, 1984, Sanderson et al. 2009) examining the pairwise geographical distributions of species pairs *within* archipelagos. Connor et al. (2013), as in previous work (Connor and Simberloff 1979, 1983, 1984, Simberloff and Collins 2010, Collins et al. 2011), followed this convention since it appeared to be part of the definition of and the tradition for inferring competitively determined checkerboard distributions. It is conceivable that one could attempt to analyze rigorously the global pairwise distributions of species, but Diamond et al. (2015) have not done so. Furthermore, such an analysis would raise new issues. For example, how should patchy distributions within larger islands like New Guinea be treated when one scores checkerboard distributions? How should the barriers to dispersal among island groups within archipelagos, as proposed by Mayr and Diamond (2001), inform the analysis?

Diamond et al. (2015) marshal only a single example to support their contention that, by analyzing the entire or global distributions of species, one would detect many pairs of species that display checkerboard distributions because of competition. Furthermore, their critique is based on the simple inspection of a map, which is tantamount to Diamond's (1975) original basis for inferring that competition had affected the geographical distribution of species: that a checkerboard distribution is prima facie evidence for competitive interactions shaping geographical distributions; in essence, checkerboards arise only because of competition. They claim that merely by visually examining the ranges of *Macropygia mackinlayi* and *M. nigrirostris* they can tell that the distribution of these two species requires an explanation involving interspecific competition—a clear case of déjà vu all over again. However, Mayr and Diamond (2001) provided compelling evidence for the existence of barriers to dispersal within archipelagoes, and barriers likely exist between archipelagoes as well. Any analysis would need to account for potential dispersal limitation both within and between archipelagoes.

Connor et al. (2013) motivated the three attributes that they claim define a "true checkerboard," a species pair that would have geographical distributions consistent with competitive interactions: (1) the pair would have exclusive island-by-island distributions, (2) their geographic ranges would overlap more than expected were they independently determined, and (3) the pair would share one or more of the island groups defined by Mayr and Diamond (2001) and mapped by Simberloff and Collins (2010) and Collins et al. (2011) for the Solomon Islands and the Bismarck Archipelago, respectively. These three criteria were intended to provide an operational definition of a "checkerboard" distribution sensu Diamond (1975) and Mayr and Diamond (2001). Diamond et al. (2015) do not object to this definition, yet as mentioned above they feel confident that their visual inspection of the ranges satisfies the second criterion. In the analysis conducted by Connor et al. (2013), the pair of Cuckoo Doves in question met

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criteria 1 and 3, but the statistical analysis showed that the overlap of the geographic hulls of these two species was in fact not statistically significantly greater than expected were the distributions determined independently. If Connor et al.'s (2013) analysis were repeated using the convex hulls for the global geographical distribution of each species, Diamond et al. (2015) would have us believe that the results would be different. While this is certainly a possibility, without actually doing the hard work of performing an analysis as did Connor et al. (2013), it remains an unsubstantiated claim. Comparing the global distributions of species pairs would not change how species pairs are scored on either criterion 1 or 3 of Connor et al. (2013). It would alter the observed scaled overlap between their convex hulls, and, commensurately, the expected overlap and its standard error. However, we doubt that an analysis based on global geographical distributions would shift the null statistical distribution of scaled overlap to such an extent that the observed overlap between *M. mackinlayi* and *M. nigrirostris*, or any other pair for that matter, would then become statistically significantly more than expected under the hypothesis that species ranges are independent (criterion 2).

Connor et al. (2013) did not include a lengthy Appendix with all the convex hulls of all pairs of species or even just the congeners and guild members, since these pictures by themselves cannot decide the issue at hand. Without the statistical analysis it is impossible to tell if any pairs of species meet the three criteria they propose to define a "true checkerboard." In particular, it is not clear from the maps shown or referenced by Diamond et al. (2015) that the geographical distributions of these species, as represented by their convex hulls, overlap more than expected were the species distributions determined independently. Connor et al. (2013) did provide the observed, expected and the standard deviation of the expected values of overlap for each pair of congeneric species and guild members in their Appendix C.

Finally, Diamond et al. (2015) are correct; Connor et al. (2013) did not include information on vagrancy. But vagrancy is not evidence of competitive exclusion. Vagrants merely indicate that individuals of a species occasionally arrive at a location but have not established a resident population that breeds and recruits. Lack of the establishment of a population could arise for many reasons other than competition, among them insufficient propagule size, lack of appropriate habitat, predators, demographic or environmental stochasticity, etc.

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