

Editorial

Avian evolution and speciation in the Southeast Asian tropics

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An emerging paradigm in analysis of geographic differentiation and speciation is integration of phylogeographic analyses and paleo-distributional projections to gain insight into these complex historical processes (Peterson, 2009). This approach hinges on the idea of a relatively stable landscape, across which species are distributed, with occasional dispersal events or climate-driven range shifts that open possibilities for population isolation and speciation (Smith et al., 2014). To date, the integration has been employed largely in single-lineage studies, such that evaluations of its effectiveness, caveats to its use, and appreciation of its strengths and weaknesses have been difficult (see early examples in Hosner et al., 2014, Lim et al., 2011, Peterson and Nyári, 2007). In this Special Column, we have assembled a group of 12 authors applying this methodology to bird taxa distributed across East and Southeast Asia and nearby islands. In this set of papers, we examined 10 avian lineages (species or complexes of species) using similar molecular and paleo-geographic analytical approaches, creating a rare comparative dataset by which to evaluate generalities underlying the process of population divergence and assess region-wide commonalities to understand historical processes impacting these lineages.

Highlights of the individual chapters are several. For both *Cyanoderma ruficeps* and *Pomatorhinus* spp., population differentiation appeared to reflect refugial conditions during the Last Interglacial (LIG) rather than the Last Glacial Maximum (LGM; Hosner et al., 2015, Reddy and Nyári, 2015), which provides further support

for deeper time origins (i.e., before the Late Pleistocene) of Asian bird species (Lei et al., 2015, Zhao et al., 2012), a pattern that has been evident in other studies, even those without a paleo-reconstruction element (e.g., Lim et al., 2011, Sheldon et al., 2009, Zou et al., 2007). Population divergence of *Copsychus saularis* and *Megalaima haemacephala* appears to have been driven by combinations of unsuitable climatic conditions and sea channels (Lim et al., 2015); similarly, *Aegithalos concinnus* and *Garrulax elliotii* reflected strong effects of isolation via climate and topography, effectively experiencing long-term *in situ* diversification (Quan et al., 2015), as proposed previously by Qu et al. (2014).

Scanning across these focal lineages, which more or less coincide distributionally across East and Southeast Asia, we noted several commonalities and contrasts. (1) *Diverse levels of genetic differentiation*—Species range from dramatically differentiated across Southeast Asia, as in the cases of *Cyanoderma ruficeps* and *Pomatorhinus* spp., down to no appreciable differentiation (at least in terms of mitochondrial DNA) whatsoever, as with *Spizixos semitorques*. (2) *Distinct island populations*—Marked differentiation of populations on Hainan and Taiwan islands is apparent in four of the five species for which island populations exist and were sampled, suggesting that levels of endemism on those islands should be reconsidered more generally (Wu et al., 2012). (3) *Frequent mixing and population overlap*—Areas on the mainland of East and Southeast Asia frequently show what appears to be mixing of differentiated populations, especially in south-central China (notable in *Cyano-*

derma ruficeps, *Paradoxornis webbianus*, *Copsychus saularis*, and *Pomatorhinus reconditus*). These characteristics appear to be shared across the set of species analyzed, although including still more lineages might flesh out their frequency and the details of their distribution.

In the paleo-distributional projections, interesting details were noted in each lineage analyzed, but some difficulty was encountered in interpreting complex patterns and distinguishing interesting signals from confusing noise. Last Glacial Maximum paleo-distribution disjunctions were noted in *Aegithalos concinnus* and *Garrulax elliotii* (both montane species), but Last Interglacial disjunctions were perhaps more common (e.g., *Cyanoderma ruficeps*, *Pomatorhinus* spp.). This mixing of different refugial time periods had been noted for this region in previous studies (Peterson and Ammann, 2013). These results also suggest more complexity in historical biogeographic processes than has been noted, for example, in similar analyses in the Amazon Basin (Bonaccorso et al., 2006; Ingenloff and Peterson, 2015; Peterson and Nyári, 2007).

An important point in exploring these possibilities in analysis and interpretation is the limited and circumscribed nature of the paleo-distributional projections. That is, such projections are presently limited to temporal ‘snapshots’ for the present-day, mid-Holocene, LGM, LIG, and (soon) Pliocene time periods (Lima-Ribeiro et al., 2015); although they likely illustrate extreme or near-extreme distributional situations in the past million or so years, no guarantee exists that time periods crucial to a given evolving lineage will coincide with these points in time for which we have climate data. For instance, in the Amazon Basin, the trumpeters (*Psophia* spp.) appear to have differentiated in response to time periods predating the Pleistocene but requiring more detail than the limited Pliocene data that are available (Ribas et al., 2012). As such, a frequent result is that the same pattern or level of disjunction in paleo-potential distributional areas may or may not be relevant to different lineages, which raises complexities in interpretation. Understanding paleo-distributional projections is further complicated by the coarse spatial resolution that characterizes all climate model outputs available for these studies (Lima-Ribeiro et al., 2015).

Southeast Asian bird lineages, at the same time, clearly show more complexity in degree of population differentiation than those in the Amazon Basin, where deep differentiation has been a constant among many studies (e.g., Aleixo, 2004; Aleixo, 2006; Aleixo et al., 2013).

That is, among the 10 taxa treated in this set of studies, differentiation ranged from essentially nil (e.g., *Spizixos semitorques*) to deep (e.g., *Pomatorhinus* spp.). The relative frequency of deep mitochondrial differentiation within and among continuously distributed populations (e.g., *Cyanoderma ruficeps*) likely reflects climate-driven, geographic processes that perhaps characterized the Pleistocene in the region (see, e.g., Alström and Olsson, 1999; Martens et al., 1999).

The resolution that is possible in studies such as those in this issue is constrained further by sampling: paleo-distribution analyses by availability of vouchered locality data and sufficient temporal snapshots of climatic conditions, and genetic studies again by availability of appropriate samples from key sites, and, at least so far, by the limited number of genetic markers employed. Future studies will benefit from increased access to geo-referenced primary occurrence data (e.g., via VertNet and GBIF), an improved partnership between the biogeography and climate modeling communities, continued detailed scientific collecting of high-quality samples from wild populations, and inclusion of more genetic markers. The large numbers of loci available from next-generation sequencing methods (Faircloth et al., 2012; Miller et al., 2007) will allow exploration of the population-genetic processes occurring in zones of contact between differentiated populations.

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