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The role of niche divergence and geographic arrangement in the speciation of Eared Pheasants (*Crossoptilon*, Hodgson 1938)

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ABSTRACT

One of the most contentious theories in current ecology is the ecological niche conservatism, which is defined as conservatism among closely related species; however, the ecological niche can also be shifted, as documented in several cases. Genetic drift and ecological divergent selection may cause ecological niche divergence. The current study aims to test whether the ecological niche is conserved or divergent and to determine the main factor that drives ecological niche divergence or conservation. We analyzed the phylogenetic relationship, ecological niche model (ENM) and demographic history of Eared Pheasants in the genus *Crossoptilon* (Galliformes: Phasianidae) to test niche conservatism with respect to different geographically distributed patterns. The phylogenetic relationship was reconstructed using ∗BEAST with mitochondrial cytochrome *b* (cyt *b*) and 44 unlinked autosomal exonic loci, and ENMs were reconstructed in MAXENT using an average of 41 occurrence sites in each species and 22 bioclimatic variables. A background similarity test was used to detect whether the ecological niche is conserved. Demographic history was estimated using the isolation with migration (IM) model. We found that there was asymmetric gene flow between the allopatric sister species *Crossoptilon mantchuricum* and *C. auritum* and the parapatric sister species *C. harmani* and *C. crossoptilon*. We found that ecological niches were divergent, not conserved, between *C. mantchuricum* and *C. auritum*, which began to diverge at approximately 0.3 million years ago. However, the ecological niches were conserved between *C. crossoptilon* and *C. harmani*, which gradually diverged approximately half a million years ago. Ecological niches can be either conserved or divergent, and ecological divergent selection for local adaptation is probably an important factor that promotes and maintains niche divergence in the face of gene flow. This study provides a better understanding of the role that divergent selection has in the initial speciation process. The platform combined demographic processes and ecological niches to offer new insights into the mechanism of biogeography patterns.

1. Introduction

Divergent natural selection, which is driven by adaptations to different ecological conditions as opposed to geographical isolation and genetic drift (both them may not cause organisms adaptation), is thought to be an important driving force that promotes the speciation process among closely related species or intraspecific populations (Rundle and Nosil, 2005; Holliday et al., 2012). By contrast, gene flow tends to homogenize divergence and thus constrains species divergence (Ford et al., 2015). However, the relative importance of selection and gene flow and their potential influences on speciation remain an open question in evolutionary biology. One challenge is to disentangle their contributions and to examine the extent to which these factors affect species diversification in varied spatial and temporal scales (Friesen, 2015). A promising framework to determine the specific role of selection and gene flow in species diversification is to investigate divergence patterns in closely related species in different geographic arrangements. For example, it is feasible to directly detect ecological niche differentiation (as a proxy of selection) and the magnitude of gene flow between allopatric and parapatric pairs of species. Using comparative geographic approaches, it is possible to infer the strength of selection in the face of gene flow.

The level of niche divergence between taxa is varied. It is often considered that the ecological niches remain unchanged among

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closely related species or conspecific populations, which is defined as niche conservatism (Holt and Gaines, 1992; Peterson et al., 1999; Wiens and Graham, 2005). This theory is invoked to understand the range limits of species and the ecological constraints on restricting the gene flow between incipient species that could promote allopatric speciation (Peterson et al., 1999). Prevalent evidence of niche conservatism has been documented in sister species pairs (e.g., Schiaparelli et al., 2015; Silva-Arias et al., 2015) and among several species within a clade (e.g., Eaton et al., 2008; Ibarra-Cerdena et al., 2014).

However, not all extant organisms showed ecological niche conservatism in empirical studies (Nyari and Reddy, 2013). Climatic and environmental changes can create ecological opportunities for organisms to adapt to novel environments and can thus cause niche differentiation and evolution. The Grinnellian niche, which is the set of abiotic variables, such as temperature and precipitation, in which a species can persist, is the most affected by climactic and environmental changes and differs from the Eltonian niche, the set of biotic conditions in which a species can persist (James et al., 1984). Ecologically based divergent selection can arise when organisms exploit a novel ecological niche (Holt and Gaines, 1992) that differs from the ancestral one. This behavior could induce shifts in phenotypic traits through phenotypic plasticity (Price et al., 2003) and genetic mechanisms (Rundle and Nosil, 2005). Although niche divergence can principally render divergence among closely related species or populations, the underlying endogenous (e.g., genetic) and exogenous (e.g., ecological) factors that can cause niche divergence remain unknown (Pyron et al., 2015).

The existence of the exclusive concept of ecological niche may be due to various temporal scales and geographical patterns when testing alternative hypotheses on ecological niche. Niche conservatism is usually predicted among closely related species that have short to moderate evolutionary histories (Peterson, 2011), e.g., between sister species (Anacker and Strauss, 2014). However, the empirical tests also show contrasting cases whereby the divergence of ecological niche evolution occurs during species radiation (Liu et al., 2016). When testing for niche divergence, a temporal scale is usually considered in a phylogenetic context, but this practice may occasionally neglect geographical arrangements of organisms, such as the study that analyzed the ecological niche of Scimitar Babblers (*Pomatorhinus*) (Nyari and Reddy, 2013). For instance, allopatric sister species could have a different ecological niche pattern from non-allopatric (parapatric or sympatric) sister species because of the cease of gene flow (Blair et al., 2013; Lee-Yaw and Irwin, 2015). Under this premise, it is necessary to consider the geographical arrangement of the study species and to evaluate their ecological niches and gene flow patterns. In other words, between allopatric sister species and parapatric ones, is the greater niche divergence in the former due to divergent natural selection or to genetic drift?

Here, we focus specifically on detecting the factors that cause the ecological niche to diverge among four species of Eared Pheasants in the genus *Crossoptilon* (Galliformes: Phasianidae). Previous studies have revealed that this genus contains two subclades: one includes White (*C. crossoptilon*) and Tibetan (*C. harmani*) Eared Pheasant, and another subclade includes Blue (*C. auritum*) and Brown (*C. mantchuricum*) Eared Pheasant (Kimball et al., 2011). *C. crossoptilon* and *C. harmani* have parapatric distributions and are mainly distributed on the Qinghai-Tibetan Plateau, whereas *C. auritum* are allopatric with *C. mantchuricum* and are distributed at the eastern edge of the Qinghai-Tibetan plateau, with an isolated

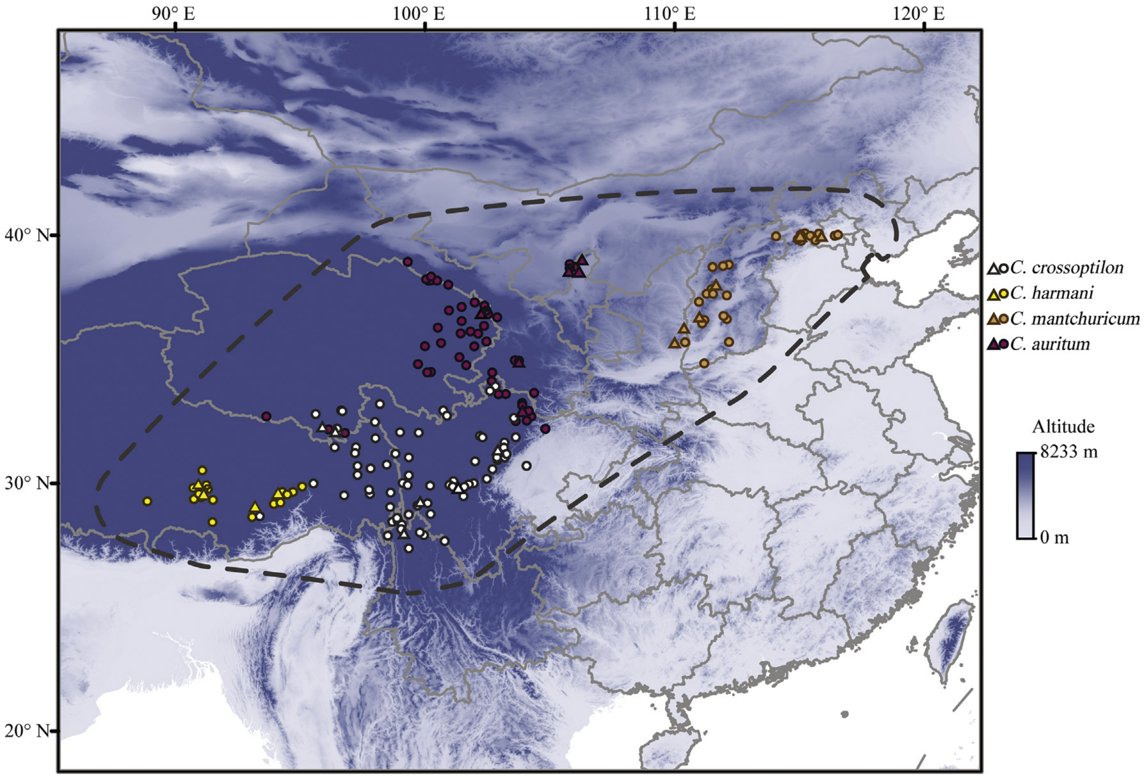

Fig. 1. Map of the study area indicating the occurrence points used in for the background similarity test of Ecological Niche Models (ENMs) and the location of DNA samples used in demographic analyses. (The occurrence points (circles) were from bird-watching records (http://birdtalker.net/), the Global Biodiversity Information Facility (http://www.gbif.org/) and our unpublished survey data. Occurrence points that were far from each other (at least 10 km) and were randomly chosen in ArcGIS software were used for the background similarity test. The study area was the minimal convex polygon of those occurrence points with an additional 200 km. Triangles represent the locations of DNA samples. The area surrounded by the black dashed line was the study area used for the background similarity test.