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NEWS AND VIEWS

PERSPECTIVE

Ring species as demonstrations of the continuum of species formation

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In the mid-20th century, Ernst Mayr (1942) and Theodosius Dobzhansky (1958) championed the significance of 'circular overlaps' or 'ring species' as the perfect demonstration of the gradual nature of species formation. As an ancestral species expands its range, wrapping around a geographic barrier, derived taxa within the ring display interactions typical of populations, such as genetic and morphological intergradation, while overlapping taxa at the terminus of the ring behave largely as sympatric, reproductively isolated species. Are ring species extremely rare or are they just difficult to detect? What conditions favour their formation? Modelling studies have attempted to address these knowledge gaps by estimating the biological parameters that result in stable ring species (Martins *et al.* 2013), and determining the necessary topographic parameters of the barriers encircled (Monahan *et al.* 2012). However, any generalization is undermined by a major limitation: only a handful of ring species are known to exist in nature. In addition, many of them have been broken into multiple species presumed to be evolving independently, usually obscuring the evolutionary dynamics that generate diversity. A paper in this issue of Molecular Ecology by Fuchs *et al.* (2015), focused on the entire genealogy of a bulbul (*Alophoixus*) species complex, offers key insights into the evolutionary processes underlying diversification of this Indo-Malayan bird. Their findings fulfil most of the criteria that can be expected for ring species (Fig. 1): an ancestor has colonized the mainland from Sundaland, expanded along the forested habitat wrapping around Thailand's lowlands, adjacent taxa intergrade around the ring distribution, and terminal taxa overlap at the ring closure. Although it remains unclear whether ring divergence has resulted in restrictive gene flow relative to that observed around the ring, their results suggest that circular overlaps might be more common in nature than currently recognized in the literature. Most importantly, this work shows that the continuum of species formation that Mayr and Dobzhansky praised in circular overlaps is found in biological systems currently described as 'rings of species', in addition to the idealized 'ring species'.

Keywords: circular overlaps, gene flow, hybridization, speciation

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The rise and fall of ring species

Ring species were famously asserted to be a perfect demonstration of speciation by Mayr (1942). At the time, Mayr was attempting to make several important points about species: (i) that they evolve, (ii) that they vary geographically, (iii) that one can make logical arguments about how geographic variation can lead to species formation and (iv) that species can form even in the presence of gene flow. The vision of ring species has long been before us, in theory, but in practice examples have been rare. This has led to a sense that ring species are an unfulfilled promise, or even worse, a wish-fulfilment fantasy. However, there are very good reasons why we have so few convincing examples.

A biological reason might be that ring species are an ephemeral manifestation of species formation. In an idealized ring species, when the distal elements of the circle meet, termini function as independent species, despite being interlinked around the rest of the circle by gene flow. This is probably unattainable except under the most extreme conditions. Climatic fluctuation will lead to population fragmentation and vicariant divergence, resulting in temporary breaks of gene flow. Few organisms will have the resilience to maintain a semblance of the original ring. Rare examples of some that have are the salamander ring species *Ensatina* (Pereira & Wake 2009) and the greenish warbler (Alcaide *et al.* 2014). With extended vicariance, ring species will eventually fall apart into multiple species and, with the extinction of key units, the complex can even lose its monophyletic nature and the original ring is no longer recognizable. Another problem is taxonomic zeal; diagnosable elements of the ring are discovered and named without regard to each other (*Ensatina* contained 4 species, described between 1850 and 1928, when Stebbins 1949, began his work), and the evolutionary pattern is not perceived. Thus, despite few examples of ring species, the deck is stacked against the perception of ring species, and we have no good idea as to how many actually exist.

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A new ring around Thailand's lowlands

Alophoixus is a monophyletic genus of birds that inhabits montane habitats of the Indo-Malayan bioregion. With a thorough sampling of the whole species complex, spanning several taxonomic ranks, Fuchs *et al.* (2015) provide important insights into the evolutionary processes underlying diversification in this system. Notably, diversification of mainland taxa is consistent with most criteria expected for ring species (Fig. 1A). First, the species tree shows that mainland taxa are monophyletic, likely descending from a single colonization from Sundaland. Second, parapatric taxa are sister in the phylogeny, suggesting that current eco-morphotypes (Fig. 1B) diverged from a stepping stone colonization of the high elevation forest around Thailand's lowlands. Current distributional gaps suggest that divergence in this species complex is not only explained by isolation by distance, but also by periods of geographic isolation that likely have occurred during the climatic cycles following initial diversification of the complex. Third, gene flow between parapatric taxa suggests that divergence and secondary contact between taxa around the ring have resulted in genetic intergradation, irrespective of whether interacting taxa are currently recognized as distinct subspecies or species. Fourth, demographic analyses indicate a recent expansion and geographic overlap of the most derived taxa, leading to closure of the ring distribution. Hybrids sampled at the terminus of the ring indicate that ring divergence has not been sufficient for complete reproductive isolation to evolve. Further geographic and genetic sampling is needed to test whether the closure of the *Alophoixus* ring has resulted in geneflow restriction greater than that observed in contacts around the ring. Importantly, if currently recognized species of *Alophoixus* had been studied independently of each other, or not all subspecies were included, the gradual nature of species formation (from phenotypically distinct subspecies with gene flow to overlapping species with rare hybridization) in the complex might not had been perceived.

Implications of the *Alophoixus* ring

The *Alophoixus* ring invites revisiting questions concerning the formation of ring species that might help identify other ring species. By modelling the topography of geographic barriers associated with a limited number of recognized rings, Monahan *et al.* (2012) showed that circular overlaps tend to form around a single geographic barrier, or multiple barriers in close proximity, and that such barriers are topographically similar. Ring diversification in *Alophoixus* occurred around Thailand's lowlands (Fig. 1A), which is 'cut' into two barriers (A and B) by a mountain chain. This corridor is colonized by one eco-morphotype (taxa 5), leading to a potential, unstudied, secondary contact at an intermediate stage of divergence ('?' in Fig. 1A). Importantly, both barriers are topographically identical to the Californian Central Valley (Monahan *et al.* 2012), which was necessary for ring diversification in the *Ensatina* salamander complex. By modelling neutral evolution of a species around a barrier, Martins *et al.* (2013) estimate that ring species can form, particularly when the termini have expanded over a large geographic area, as observed in

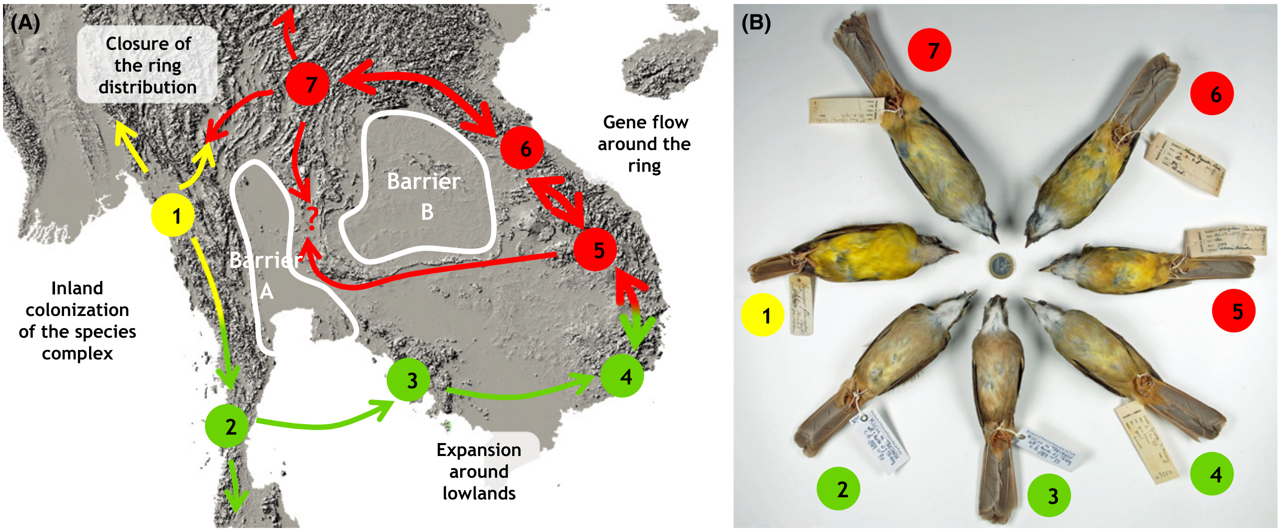

Fig. 1 Ring divergence in *Alophoixus* bulbuls. (A) Four criteria for ring species formation demonstrated in Fuchs *et al.* (2015). Taxa composing the *Alophoixus* ring are represented by circles (colours distinguish currently recognized species); single arrows represent colonization around the barrier; double arrows represent zones of genetic intergradation; question mark signs a potential secondary contact at mid-ring divergence. (B) Eco-morphotypes around the ring distribution (Photo credit: A. Previato, MNHN): (1) *A. flaveolus* (MNHN CG 1892–795); (2) *A. ochraceus ochraceus* (MNHN CG 1989–90); (3) *A. o. cambodianus* (MNHN CG 1989–89); (4) *A. o. hallae* (MNHN CG 1928–482); (5) *A. pallidus khmerensis* (MNHN CG 1929–1220); (6) *A. p. annamensis* (MNHN CG 1929–1215); and (7) *A. p. henrici* (MNHN CG 1936–736).

Alophoixus. Yet, they also estimate that ring species are likely to break up into independent species or collapse into a single species in ~130,000 generations, which is a relatively short period of time in the history of species complexes for ring species to be observed. This raises the importance of the rare, but precious, examples of circular overlaps described in the literature that maintain a semblance of the original ring, such as the *Ensatina* salamander, the greenish warblers and this new ring in *Alophoixus* bulbuls.

A century after the publication of the Origin of Species, Dobzhansky (1958) wrote 'It is no exaggeration to say that if no instances of uncompleted speciation were discovered [. . .] we would have to conclude either that evolution did not occur or that the formation of new species is instantaneous. What is a difficulty to the cataloguing systematist is a blessing to the evolutionist.' The work of Fuchs *et al.* (2015) precisely illustrates species in the making and demonstrates that the continuum of species formation can be observed within a single biological system.

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