Pleistocene range dynamics and episodic rarity in an extinct bird

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In an influential report in the field of conservation biology, Rabinowitz et al. (1) described seven ways in which species may show rarity, based on different combinations of range size, ecological amplitude, and local abundance; this paper has guided many avenues of thought in the field of conservation biology. To a conservation biologist in the 17th century, however, the passenger pigeon (Ectopistes migratorius) would not have qualified as “rare” under any of the seven categories; quite simply, the species had a broad range (eastern North America), was not particularly limited to any one set of conditions, and was massively locally abundant. Still, this species disappeared entirely by the early 20th century for reasons that have never been entirely clear. A report in PNAS by Hung et al. (2) sheds an initial glimmer of insight into this question.

Hung et al. (2) took advantage of two new capabilities: robust historical demographic inferences based on information from across the genome, and estimates of geographic potential at the last glacial maximum (LGM) based on ecological niche models. Hung et al.’s demographic inferences were based on sequences of well over half of the genome (0.74–0.99 of a genome of likely about 1.30 gigabases) of three individuals, thus being based on variation across massive numbers of genes; they used coalescent sampling (3) to estimate genetically effective population size \( (N_e) \) and sequentially Markovian coalescent analyses (4) to assess changes in population size through time. These procedures yielded estimates that indicated an \( N_e \) orders-of-magnitude smaller than that expected from the massive numbers of individuals that made up this species (3–5 billion). Hung et al.’s niche model projections—in effect calibrating models based on known occurrences of the species, and transferring those models to LGM conditions—suggested extremely restricted LGM distributional potential, such that the species was likely confined to microrefugia at various points in the Pleistocene. The combined picture is one in which populations of a species that likely ranked among the most abundant vertebrates on Earth could crash and the species go extinct extremely quickly. Most likely, the species had a “boom and bust” population biology that was sent out of its usual cycling by additional human pressures in the 19th and early 20th centuries.

This study exemplifies an important “next step” in biogeography and species-level biogeography: seeking consensus among independent data realms (5). That is, demographic inferences from phylogeographic data represent a signal from a single data stream (genomic variation) that provides rich and previously inaccessible information about population history (6); although novel, these inferences are nonetheless assumption-laden and are often presented without independent corroboration, and much discussion has centered on their parameterization and calibration (7). Clearly, these approaches offer rich insights, but methods will continue to evolve and improve, and results will improve dramatically when independent analyses and data streams yield coincident outputs.

Niche-modeling paleo-projection approaches offer such an independent data stream to complement the molecular sequence results (8, 9). These models are based on the relationship between known occurrences in the present (or, in the case of passenger pigeons, in the 19th and early 20th centuries) and climate to estimate the niche, which is in turn transferred to LGM climate conditions as estimated from general circulation model outputs. Niche-model paleo-projections presented by Hung et al. (2) corroborated in a general sense the pattern of pronounced populational and distributional fluctuations, with LGM estimates showing potential distribution only in a few very restricted parts of eastern North America. In this very general

Fig. 1. Illustration of the dramatic environmental changes affecting the geographic distribution of the passenger pigeon (Ectopistes migratorius), in which most of the known distribution of the species was covered by ice sheets at the LGM. Occurrence data (yellow triangles) were drawn from VertNet (www.vertnet.org) and LGM vegetation distributions (20) are shown with current political boundaries overlaid; LGM coastlines are shown as the limit of shading, generally somewhat more extensive than current coastlines.
sense, the coincidence between the two analyses is satisfying and convincing.

Some room for caution exists, though, as regards the paleo-distributional estimates for the species. The refugia that were identified were in western British Columbia, southern California and Arizona, southern Texas, a spot on the Atlantic coast, and a restricted area in the Great Plains: quite a variety of environmental situations and not a particularly cohesive picture of the potential distributional ecology of the species at the LGM. Indeed, the two western refugia probably fall outside of the accessible area (M) of the species (10), and thus would be irrelevant to the LGM distributional history of the species. The Great Plains and coastal refugia look more like artifacts of extrapolation of niche models, which have complicated previous such projections: consider, for example, the illusory niche shifts in invasive plants (11) and ants (12) that disappeared with more detailed analysis (13). Indeed, my suspicion is that the only meaningful refugium identified by Hung et al. (2) is that of southern Texas, and that that refugial area was probably more extensive but appears small for methodological reasons; see the relationship between passenger pigeon distributional patterns and LGM vegetation patterns in Fig. 1. Very simply, ecological niche-model transfers are not easy and require quite a bit of experimentation to get them to work robustly (14).

For both of these new methodologies, not only has considerable progress been made, but considerable progress still remains to be made. For example, the assembly of the genome of this extinct bird species was possible (or at least was made much easier) thanks to the availability of the full rock dove (Columba livia) genome (15), although some de novo assembly was conducted (16). Clearly, as the density of reference genomes improves, so also will the facility of development of such special genome sequences (think Carolina parakeet, Conuropsis carolinensis, as an exciting possibility) as was achieved by Hung et al. (2).

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On the niche-modeling and paleo-distributional projection side, similar major challenges remain. Current paleo-climate data are rather horrifyingly coarse in spatial resolution (~300 km), and any use of these data depends crucially on rather simple techniques for downsampling to more meaningful spatial resolutions. What is more, at present, views of paleo-climatic conditions are very limited: data for 6,000 y before present, LGM (20,000 y before present), and last interglacial (135,000 y before present) are readily available, and one transient model of the last deglaciation (17) and Pliocene (~3.5 Mya) models (18) are becoming available. Clearly, greater density of climatic datasets through time from more modeling centers will make these paleo-distributional explorations far more robust (19).

In sum, Hung et al. (2) present a fascinating first view of the paleo-demography and paleo-distribution of passenger pigeons, and offer novel insights into reasons behind the species’ extinction. The insights gained suggest an eighth form of rarity for the classification of Rabinowitz et al. (1): wild population fluctuations that may be cloaked by current large populations, but that may place certain species at greater risk of extinction. More generally, clearly the fields of biogeography, macroecology, and conservation biology will benefit enormously as these new analytical capabilities continue to develop and mature.