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Estimating extinction risk under climate change: next-generation models simultaneously incorporate demography, dispersal, and biotic interactions

Estimating species-level extinction risk under projected future climate change is challenging. About ten years ago, Chris Thomas and colleagues used correlative species distribution models (SDMs) and future climate scenarios to estimate extinction risk for >1100 animal and plant species (Thomas et al. 2004). They predicted that 15–37% of their sample species will be 'committed to extinction' by 2050. The validity of such results is highly questionable because implausible assumptions in correlative SDMs introduce large unknowns into extinction risk forecasts (e.g., Dormann 2007). For example, a key assumption is that species' distributions are at equilibrium with climate and that observed correlations with climate will extend into the future. A further limitation is that population-level processes such as demographic rates, dispersal distances, and antagonistic or mutualistic interactions among species are not incorporated into SDMs (e.g., Hampe 2004). Nevertheless, recent biogeographical research may finally resolve some of these outstanding challenges (Kissling et al. 2012, Schurr et al. 2012, Travis et al. 2013, Wisz et al. 2013).

In a groundbreaking addition to this growing area of research, Fordham et al. (2013) provide a framework for a next-generation model which simultaneously incorporates demography, dispersal, and biotic interactions into estimates of extinction risk under projected climate change. The authors apply this model to one of Europe's most endangered mammals, the Iberian lynx (*Lynx pardinus*), which is restricted to isolated populations in southwestern Spain. The modeling framework (Figure 1) is centered on demographic (metapopulation) simulations for the Iberian lynx and the European rabbit (*Oryctolagus cuniculus*), the latter being the main food source of the lynx. Metapopulation models were implemented as age- and sex-structured models for the Iberian lynx (with age and sex specific survival rates and

fecundity estimates for age of reproduction, litter size, etc.) and as scalar type stochastic models for the rabbit (to estimate population growth rates without the need to include population age or stage structure). For both species, outputs from correlative SDMs (in annual time steps from 2000–2100, using ensemble projections based on seven different SDM methods, seven climate change models, and two emission scenarios) were only used to estimate the carrying capacity for the demographic models. In other words, they were used as spatial layers describing climate suitability, i.e. as one of the components of habitat suitability for the two species (Figure 1). The coupling of SDMs with demographic models is a recent advance (Keith et al. 2008), and represents a major step forward in predicting species-level extinction risk under climate change.

Dispersal for both species is modelled using functions to determine the proportion of each population that disperses between grid cells or subpopulations (Figure 1). For the lynx, a declining function between subpopulations was used for distances up to 45 km; the maximum dispersal distance which has been empirically reported for this species. Furthermore, a remotely-sensed map (CORINE) was used to identify land cover types with different degrees of suitability for lynx dispersal (from very good to highly unsuitable). Lynx dispersal was assumed to be stage-specific (young individuals versus adults) and density dependent (based on number of breeding-age individuals in a population), allowing for more detailed simulation of movement. For rabbit dispersal, a declining function up to a maximum dispersal distance of 15 km was used, closely approximating a 1% movement at distances of >3 km. Dispersal and movement data for both species were based on previously published studies, highlighting the utility of empirical estimates of maximum dispersal distances, movement behavior and habitat selection

in heterogeneous and fragmented landscapes.

In contrast to previous correlative SDMs and coupled SDM-metapopulation models, Fordham et al. (2013) also incorporated biotic interactions into their framework (Figure 1). The chosen interactions reflected a bi-trophic predator-prey interaction between the Iberian lynx and the rabbit. Specifically, the simulated spatially-explicit (and temporally changing) densities of the rabbit enter as prey abundance estimates into habitat suitability predictions for the Iberian lynx. Rabbit densities were based on simulations that integrate climate suitability (estimated from SDMs), land cover (unsuitable, highly productive, and unproductive rabbit habitats), dispersal (see above), and disease dynamics (myxomatosis and rabbit haemorrhagic disease, RHD) (Figure 1). More complex simulations of predator-prey dynamics, such as those linking Iberian lynx survival and fecundity to rabbit abundance), were not possible because of the lack of empirical data on which to base the functions.

It is important to remember that even with such complex and data-intensive models, a number of limitations and uncertainties remain. First,

a key assumption in the Fordham et al. (2013) study is that the spatial distribution of land cover types and their habitat selection by both species will remain constant. However, it is unlikely that land cover will be unchanged at the end of the current century and large uncertainties inherent in projections of land use change severely limit the precision of future land cover scenarios (Millennium Ecosystems Assessment 2005). Moreover, it is unclear to what extent the habitat of both lynx and rabbit will change and whether the observed niche of both species will be conserved under global change (Wiens et al. 2010). Second, there is currently very little information available about disease dynamics under climate change. The probability of Feline Leukemia Virus (FeLV) was included in the Iberian lynx demographic simulations (Figure 1) through a decrease in survival rates, specifically as a population catastrophe occurring at a rate of 1 in 40 years. For the rabbit, myxomatosis was included within environmental stochasticity while RHD was explicitly modeled via an estimated 15–25% reduction in rabbit abundance every 2–3 years (Figure 1). Whether the frequency and magnitude of such disease out-
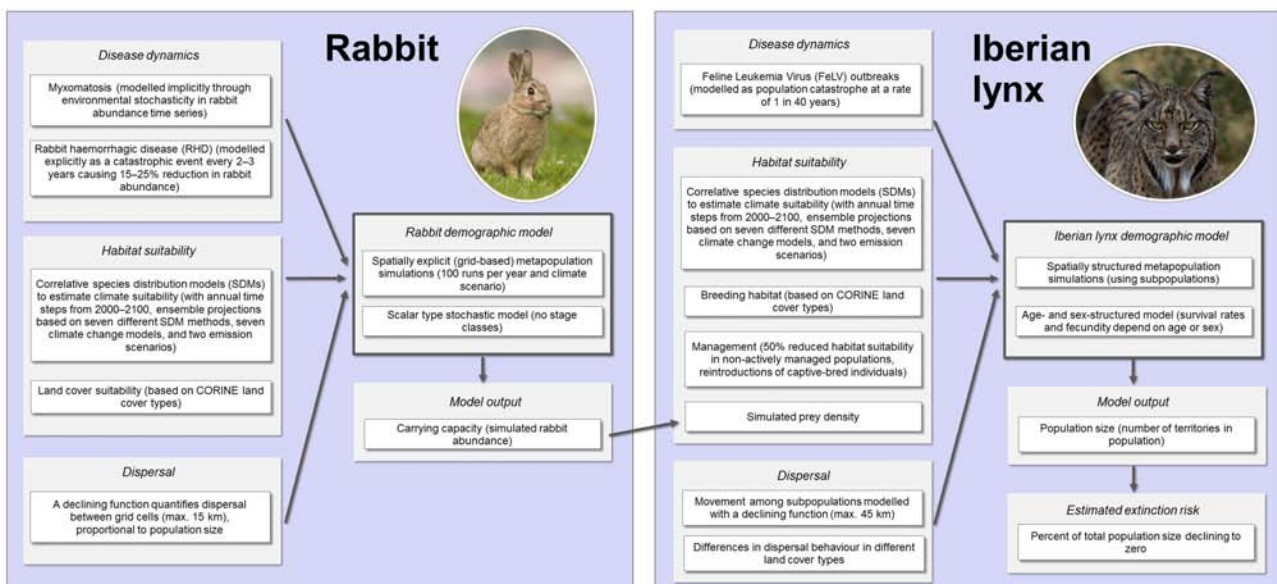

Figure 1. Schematic overview of the modeling framework used by Fordham et al. (2013) to estimate extinction risk of the Iberian lynx (*Lynx pardinus*) under projected future climate change. This modeling framework implements demographic (metapopulation) models for the Iberian lynx and its main prey, the European rabbit (*Oryctolagus cuniculus*), together with estimates of disease dynamics, habitat suitability, and dispersal. The main implemented biotic interaction reflects a bi-trophic predator-prey interaction between the Iberian lynx and the rabbit, with simulated rabbit abundances entering as prey density into habitat suitability estimates of the Iberian lynx. Images are derived from Wikicommons via Creative Commons (rabbit photo from J. J. Harrison, lynx photo from www.lynxexsitu.es).

breaks is realistic under climate change remains uncertain. Third, a major limitation for extending the model framework to other species is the general lack of comprehensive empirical data on demographic rates, dispersal, and biotic interactions for many species. The highly specialized feeding niche of the Iberian lynx allowed a unidirectional, bi-trophic interaction to be incorporated into the extinction risk projections. However, the majority of species are embedded into more complex networks of interacting species and a deeper understanding of unidirectional and reciprocal multispecies interactions is urgently needed (Kissling et al. 2012). Moreover, the lack of empirical data on large-scale variation in demographic responses (e.g., survival, fecundity or growth), especially in age-, size-, or stage-structured populations (Schurr et al. 2012), currently prevents the expansion of such complex modeling frameworks to most other species.

Nevertheless, the main focus of Fordham et al. (2013) was not on methodological advancements. Rather, the authors aimed to assess extinction risk of the Iberian lynx under climate change for three possible management scenarios: present-day conservation practices, regional reintroductions of captive-bred Iberian lynx, and peninsula-wide reintroductions. Their complex, cutting-edge simulations suggest that the world's most endangered cat species is likely to go extinct within the next 50 years in the absence of carefully planned reintroduction programs. Despite this unoptimistic prognosis, the modeling framework itself is an important step forward in our ability to assess extinction risk of select species under climate change. Hopefully, it will encourage the collection of new data on demographic rates, movement behavior, antagonistic and mutualistic interactions, habitat selection, and disease dynamics. It also highlights the need for the urgent development of more complex models than the classical correlative SDMs that can provide more realistic and rigorous scientific guidance for policy and conservation management in the 21st Century.

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