Demography as the basis for understanding and predicting range dynamics

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Demographic processes and demographic data are increasingly being included in models of the spatio–temporal dynamics of species’ ranges. In this special issue, we explore how the integration of demographic processes further the conceptual understanding and prediction of species’ range dynamics. The 12 papers originate from two workshops entitled ‘Advancing concepts and models of species range dynamics: understanding and disentangling processes across scales’. The papers combine theoretical and empirical evidence for the interplay between environmental conditions, species interactions, demographic processes (births, deaths, dispersal), physiology, and evolution, and they point out promising avenues towards a better understanding and prediction of species’ range dynamics.
demography as the basis for range dynamics

Why focus on demography? From a demographic viewpoint, the range dynamics of species is best understood by how fundamental demographic processes (e.g. death, birth and dispersal) of individuals are influenced by abiotic and biotic conditions and how evolution and ecophysiology influence these processes and thus population dynamics across time (Sexton et al. 2009, Schurr et al. 2012, Schiebers et al. 2014, Snell et al. 2014, Svenning et al. 2014). Focusing on demography thus provides a natural link between multiple factors and processes, because demographic changes relate to the spatial and temporal expression of the niche caused by environmental and evolutionary drivers (Holt 2009, Schurr et al. 2012, Merow et al. 2014a, Thuiller et al. 2014a). Moreover, a demographic approach to understanding and predicting species’ range dynamics has the advantage of being rooted in ecological theory.

The foundations for this theory were laid by Hutchinson (1957) who defined the ecological niche as the set of all environmental conditions under which a species can persist indefinitely. Subsequently, Maguire (1973) cast this definition in demographic terms by pointing out that (for simple population dynamics) the niche consists of all environments in which the intrinsic population growth rate is positive ($r > 0$ in the absence of dispersal) because reproduction outweighs mortality. One might thus expect that a species’ geographical range directly reflects its niche by comprising all areas in which the environmental conditions allow populations to persist. However, several factors might cause species to be absent from environmentally suitable conditions or to be present at environmental unsuitable conditions. This mismatch can have several reasons. Firstly, repeated dispersal of individuals from populations in favorable conditions (sources) can maintain populations at environmentally suboptimal sites (sinks; Pulliam 2000, Holt et al. 2005). Secondly, in changing environments, populations may temporarily persist even though their present-day growth rate is negative because environmental conditions have deteriorated. Thirdly, species might be excluded from suitable sites by superior competitors (Meier et al. 2010, 2011, Pellissier et al. 2010) or they might fail to colonize all suitable sites (Pulliam 2000, Holt et al. 2005). Such dispersal-related absences can be understood in the frame of meta-population dynamics (Holt et al. 2005, Schurr et al. 2007, Lester et al. 2007), or can be caused by historically time-lagged dispersal dynamics. The latter might occur after speciation (Paul et al. 2009) or in response to past climate change, such as during the Quaternary glacial-interglacial oscillations (Svenning et al. 2008, Essl et al. 2011, Normand et al. 2011, 2013).

While species distribution models (SDMs) have proved very useful for exploring determinants of species occurrences and for the development of hypotheses about the causes of the above mentioned mismatch between species geographical distributions and their niche (Normand et al. 2011, Boulangeat et al. 2012, Merow et al. 2014b), they offer limited insight into the complexity of species range dynamics, as they cannot represent the processes causing the mismatches. Suitability-based demographic models (or hybrid SDMs) attempt to account for this by linking probability of occurrence and range-wide variation in demographic parameters has not yet been tested. Thuiller et al. (2014a, this issue), examine the validity of this link and provide the first large scale assessment of the relationship among demographic parameters (intrinsic growth rate, $r$; carrying capacity, $K$) and species probability of occurrence as estimated from SDMs. Specifically, they investigate the relationship for 108 temperate forest tree species in four regions of the world. They find that most of the analyzed populations occur in areas with positive intrinsic growth rate and thus occur within the defined limits of their ecological niche. Most importantly, however, and in contrast to the expectations, their results suggest that species’ probability of occurrence is high in areas with slow population growth. This cautions against the use of probability of occurrence as a predictor of demographic parameters as often done in suitability-based demographic models. These relationships should be further tested on other life forms, in other biomes, and in relation to occurrence probabilities from simple versus complex SDMs (cf. Merow et al. 2014b). Merow et al. (2014b, this issue) preliminarily suggest that simple SDMs may be preferable in suitability based demographic models as a clear hypothesis for the link between occurrence probability and demographic parameters is important. Merow et al. (2014b) furthermore provide an important and thorough discussion of the role of SDM complexity (defined as the shape of the inferred occurrence–environment relationship) for studies of species ranges and niches. They conclude that combined insight from simple and complex SDM approaches will generate the most accurate hypotheses of occurrence–environment relationships and the potential role of interacting processes and thus facilitate the development of the next generation of range dynamic models.

underlying range dynamics

It remains an unresolved question how different limiting factors (abiotic as well as biotic) and ecological (population demography, ecophysiological) and evolutionary processes combine to influence species range dynamics. Several of the papers in this special issue provide perspectives on different drivers of variation in demographic parameters (Merow et al. 2014a, Snell et al. 2014) and on how the interplay of biotic interactions, dispersal and other demographic parameters, as well as evolutionary processes influence species range dynamics (Travis et al. 2005, Bocedi et al. 2014b, Dytham et al. 2014, Schiebers et al. 2014, Snell et al. 2014, Svenning et al. 2014). The role of biotic interactions for range limits have been the focus of several recent reviews and modelling studies (Kissling et al. 2011, Meier et al. 2012, Linder et al. 2012, Wiss et al. 2013, Araújo and Rozenfeld 2014). However, the
interplay between biotic interactions and range expansion has received little attention. Svenning et al. (2014, this issue) review theory and empirical evidence about the importance of interspecific interactions for range expansion. Theoretically, interspecific interactions can affect range expansion rates by altering local population growth or dispersal. By synthesizing available evidence, Svenning et al. (2014) show that interspecific interactions could have large effects on range expansion rates; but they also highlight that the general importance of these effects remains unknown and requires more investigation. Furthermore, Svenning et al. (2014) discuss how interspecific interactions could be integrated into models of range dynamics and provide key guidelines for when this is particularly important.

The role of complex dispersal behaviour and landscape structure is the focus of Bocedi et al. (2014b, this issue). Species’ spread has often been modelled using fixed dispersal kernels, while the role of density-dependent emigration rates, movement patterns and settlement rules have received less attention. Using a novel spatially-explicit, individual based model, which integrates complex population dynamics and dispersal behavior (RangeShifter, Bocedi et al. 2014a), Bocedi et al. (2014b) investigate the spread of animals through simulated landscapes of different complexity. They show that depending on interactions between species’ dispersal behaviour and landscape characteristics, increasing the number of suitable patches does not necessarily maximize spread rates. Their results provide clear motivation for work that models species’ range shifts using more complex representations of the dispersal process.

Landscape structure and its importance for evolutionary adaptation at the range margin is the focus of Schiffers et al. (2014, this issue). As noted above, both ecological and evolutionary processes shape species’ ranges (Sexton et al. 2009) and understanding the drivers of evolutionary adaptation is critical for predicting dynamics at range margins. Schiffers et al. (2014) tackle this important question by investigating how landscape structure interacts with the genetic architecture of the evolving trait to determine the speed of adaptation. They show that adaptation is faster when the coarseness of the trait’s genetic architecture matches the coarseness of the environment. Dispersal modifies this relationship as it determines the actual environmental coarseness experienced by a species. Schiffers et al. (2014) use ALADYN – a spatially explicit, allelic modelling framework for their simulations of joint allelic and demographic dynamics. ALADYN is freely available and its functionalities and use is described in the software note by Schiffers and Travis (2014, this issue).

Dytham et al. (2014, this issue) further explore the interplay between ecological and evolutionary processes during and after environmental change. Specifically, they use an individual-based model where population dynamics are an emergent property of resource availability and the genetically determined life-history of individuals. In the model, genes control whether an individual is semelparous or iteroparous and determine how dispersive an individual is. The model is used to explore which eco-evolutionary processes matter most during range expansion. Spatial sorting for both increased dispersal and a semelparous life-history on an expanding front result in accelerating rates of spread. Importantly, at least in these simulations, sorting of existing genetic variation is more important than the contribution of novel mutations arising during range expansion. Furthermore, their theoretical results indicate higher extinction risk when inter-individual variability prior to the start of expansion is low, and that erosion of inter-individual variability during a range-shift can depress population abundance for a long time after climate change. The theoretical results of Dytham et al. (2014) suggest that predictions of range expansion rates might be systematically wrong if inter-individual variability and resource allocation strategies are not accounted for. They acknowledge the current challenges of using this modelling strategy in real ecosystems and highlight that an ambitious research agenda combining experimental work, sampling and monitoring across large-scale environmental gradients of populations and the variation in life-histories found within and between populations, is needed for the future.

Advancing models of species range dynamics

Recently there have been many methodological, theoretical and conceptual improvements that have aimed at bringing more biological realism into models of species range dynamics (Engler and Guisan 2009, Midgley et al. 2010, Pagel and Schurr 2012, Dullinger et al. 2012, Nenzén et al. 2012, Bocedi et al. 2014a, Merow et al. 2014a). With respect to incorporating demography there are three main approaches: 1) explicit representation of demographic parameters, processes and interactions in process-based models, e.g. dynamic vegetation models (Snell et al. 2014), 2) use of demographic data as input for statistical models that predict range dynamics from demographic processes (Pagel and Schurr 2012, Schurr et al. 2012, Merow et al. 2014a), 3) suitability-based demographic models or hybrid SDM models – which link species probability of occurrence with demographic processes.

In response to point one above, Snell et al. (2014, this issue) provide an interesting synthesis of the challenges and advantages of using dynamic vegetation models to model species range dynamics. Dynamic vegetation models use a process-based approach to simulate plant population demography and interactions. Snell et al. (2014) highlight several potential avenues for further increasing the potential of dynamic vegetation models for predicting range dynamics, namely a better mechanistic representation of dispersal and other demographic processes (reproduction, seedling stage) as well as trait variability. Finally, they discuss the use of up-scaling to overcome the main limitation of the application of dynamic vegetation models for predicting range dynamics, namely the models’ complexity and its associated computational demand.

Dynamic range models (Schurr et al. 2012) or demographic distribution models (Merow et al. 2014a, this issue) use demographic data to statistically estimate demographic models from data to simulate species’ range dynamics. Merow et al. (2014a) use integral projection models (IPMs, Merow et al. 2014c) to understand environmental drivers of range-wide demographic variation in an over-story perennial shrub in the Cape Floristic region and to project its popula-
Although Merow et al. (2014a) illustrate that relatively little data is needed for building demographic distribution models and despite of demographic data becoming increasingly available (COMPADRE Plant Matrix Database, <www.compadre-db.org/>; Global Population Dynamics Database, <www3.imperial.ac.uk/cpb/databases/gpdd>), these models are still only possible for the comparably few species for which the spatial coverage of samples across a species’ range is sufficient. This calls for directed sampling efforts of demographic parameters across species ranges – an effort which would strongly profit from standardised and coordinated sampling of demographic parameters (cf. Fraser et al. 2013).

A shift from a species-specific to a trait-based approach as in biogeography and community ecology (Violle et al. 2014), might provide an important possibility for future demographic models of species range dynamics. Adler et al. (2014) report a relationship between functional traits and plant life history strategies and their associated demographic parameters, i.e. survival, growth and fecundity. Demographic distribution models on groups of species with similar traits could thus provide a promising first step. Using a suitability-based demographic model on plant functional types Boulangeat et al. (2014a, 2014b) provide an example in this direction. However, further development of this avenue warrants more tests of the relationship between occurrence probability and demographic parameters (Thuiller et al. 2014a), and currently a direct demographic approach might provide a more promising avenue (Schurr et al. 2012, Merow et al. 2014a).

On the whole, the papers in this special issue illustrate that demography provides a link between many current modelling approaches and underlines that we should work toward approaches that can integrate the interplay between environmental conditions, species interactions, demographic processes (births, deaths, dispersal), physiology, and evolution. The presented modelling approaches, and in particular the recent convergence between simple and complex approaches (Merow et al. 2014a, b, Snell et al. 2014) point out promising avenues towards such an integration and thus towards a better understanding and prediction of species’ range dynamics.

**Acknowledgements** – The papers in this special issue arose from two workshops entitled “Advancing concepts and models of species range dynamics: understanding and disentangling processes across scales”. Funding was provided by the Danish Council for Independent Research – Natural Sciences (grant no. 10-085056 to SN). We are very thankful to the many authors for their excellent contributions as well as to J.-C. Svenning (Editor-in-Chief of this issue) and M. Persson for their immense work related to editing and managing this special issue.

**References**


