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Article in *Journal of Ecology* · March 2016

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DEMOGRAPHY BEYOND THE POPULATION

Demography beyond the population

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Summary

1. Population ecology, the discipline that studies the dynamics of species' populations and how they interact with the environment, has been one of the most prolific fields of ecology and evolution. Demographic research is central to quantifying population-level processes and their underlying mechanisms and has provided critical contributions to a diversity of research fields. Examples include the spread of infectious diseases, eco-evolutionary dynamics and rapid evolution, mechanisms underlying invasions and extinctions, and forest productivity. As the fates of individual organisms are influenced by, and subsequently underlie, many other patterns and processes, we suggest that connecting demography *beyond* the population level offers promising avenues of innovation in ecology and evolution.

2. Under the premise that population-level processes are an ideal common currency within ecology and evolution, we organized the British Ecological Society Symposium, *Demography Beyond the Population*. This event attracted international researchers who are applying demographic theory and approaches to a broad range of questions. This special feature builds off of the symposium and illustrates the ability of demography to connect across diverse research areas in ecology and evolution, including functional traits, transient dynamics, quantitative genetics, environmental drivers and feedbacks, land management and other topics. In addition to highlighting the contributed manuscripts, this editorial provides a brief background on the development of the discipline and suggests how demographic tools may be used in novel ways to study more than *just* populations.

3. *Synthesis*. This special feature integrates novel lines of research in the vast field of demography that directly interact with other ecological and evolutionary disciplines. The cross-disciplinary potential of demography is further emphasized by the fact that its 20 manuscripts are spread across all six journals of the British Ecological Society. Together, these articles highlight that there is much to be gained by linking demography to other disciplines and scales in ecology and evolution.

Key-words: animal population ecology, comparative biology, demography, eco-evolutionary dynamics, functional traits, infectious diseases, integral projection models, matrix population models, plant population and community dynamics, range dynamics

Introduction

Demographers have long been intrigued by the interactions of conspecific individuals and their resulting dynamics. Fundamental ecological and evolutionary research has emerged

from this focus, informing our current understanding of density-dependence (Goldberg *et al.* 2001; Turchin 2003; Churcher, Filipe & Basáñez 2006), infectious disease dynamics (Anderson & May 1985; Grenfell & Dobson 1995), the management of invasive and threatened species (Silvertown, Franco & Menges 1996; Morris & Doak 2002; Baxter *et al.* 2006), and the evolution of life-history strategies (Childs *et al.* 2004; Salguero-Gómez *et al.* 2015a), to mention a few. However, demography is but one focal point within the broad lens of ecology and evolution, which together encompass a considerable range of scales across space, time and biological

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This article forms part of the British Ecological Society journals' Demography Beyond the Population special feature http://wileyonlinelibrary.com/BES_demography

organization (Levin 1992). Over the last century, specialization of subdisciplines has coincided with substantial advances in areas as diverse as genomics, ecophysiology, phylogenetics, community ecology and behavioural ecology. Yet, this collective endeavour has inherent limitations without adequate bridges across scales (Chave 2013). Along with focused disciplinary work, we must also pursue quantitative connections across ecology and evolution using flexible frameworks and common metrics. Demography has much to offer in this regard.

Population ecology seeks to understand the drivers of changes in abundance over time and space, with demography more specifically related to how underlying vital rates (survival, growth, reproduction, etc.) structure populations. Variation in these vital rates represents a key filter that underlies and connects many aspects of ecology and evolution (McGraw & Caswell 1996; Metcalf & Pavard 2007). These processes can be considered as a biological ‘common currency’, which are arguably situated near the middle of several scaling axes (Fig. 1). Moreover, demography is inherently a scaling tool, translating the fates of individuals into population-level outcomes. By expanding the boundaries even further, one can treat demographic metrics as predictor or response variables that link to other scales, promoting concision of ecological and evolutionary subdisciplines (Fig. 1).

Motivated by recent research that expands the disciplinary boundaries of population ecology, we (with C.J.E. Metcalf and D.Z. Childs) organized the British Ecological Society Symposium: *Demography Beyond the Population* (24–26 March 2015, Sheffield, UK). The symposium brought together a broad range of researchers using demographic theory and approaches in innovative ways. The resulting special

feature highlights these avenues of research and mirrors its bridge-building nature as the first to span across all journals of the BES: *Journal of Ecology*, *Journal of Animal Ecology*, *Journal of Applied Ecology*, *Functional Ecology*, *Methods in Ecology and Evolution*, and *Ecology and Evolution*. Our goal is to urge both demographers and non-demographers alike that there is much to be gained by linking demography to other disciplines and scales in ecology and evolution.

Populations and demography in ecology and evolution

Ecology and evolution are deeply rooted in population biology and demography. Indeed, the factors that determine the rates of population increase or decline and the differential contributions from individuals are central to evolution by natural selection. This link between individual variation and differences in survival and reproduction is also the basis of structured populations, a topic that resides at the very core of demography (Leslie 1945; Tuljapurkar & Caswell 1997; Caswell 2001). Early pioneers of theoretical ecology included Lotka (1924) and Volterra (1926), whose coupled population models of species interactions have become part of the bedrock of community ecology. Broad advances in many areas of animal ecology in the mid-20th century, such as life-history evolution (e.g. Cole 1954) or species coexistence (e.g. MacArthur 1958), were strongly influenced by the examination of population-level processes. Indeed, Hutchinson’s (1957) classic paper formalizing the concept of the ecological niche emerged from the Cold Spring Harbor Symposium entitled *Population Studies: Animal Ecology and Demography*. In the latter half of the 20th century, plant ecologists began to

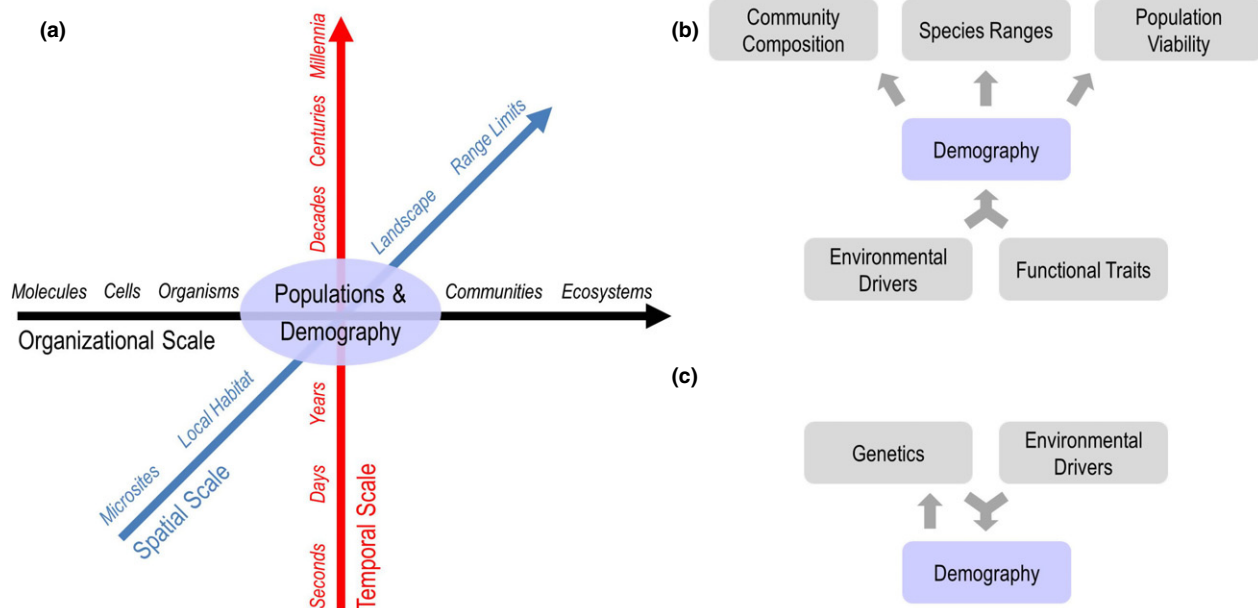


Fig. 1. (a) Populations and demography are situated near the middle of several scaling axes and can serve as a filter connecting diverse ecological and evolutionary processes. There are many opportunities for demography to inform – and be informed by – processes in different research areas and/or at variable scales, including (b) translating factors that affect individual organisms into a range of larger-scale outcomes or (c) capturing eco-evolutionary processes that involve the dynamic feedback system of genetics, environment and demography.

increase their focus on the fates of individuals and the use of population-level methods, (re)opening avenues of inquiry that were previously hindered by a largely ‘vegetationalist’ approach (Harper 1967). Today, plant and animal ecologists are starting to blur taxonomic lines, using many shared frameworks and methodologies with population-level origins.

Many of the theoretical population models that helped to advance ecology in the early 20th century did not explicitly consider population structure, a key focus of demography. This limitation was directly addressed with the rise of matrix population models (Leslie 1945; Lefkovich 1965), which can describe the population dynamics of virtually any life history that can be represented with discrete classes. The further development of analytical tools (e.g. Tuljapurkar & Orzack 1980; de Kroon *et al.* 1986; Caswell 1989; van Groenendael *et al.* 1994) coincided with a tremendous increase in the use of empirical structured population models in ecology over the last two decades. By the 1990s, matrix population models had become one of the most frequently used methods to translate vital rates into population-level outcomes, allowing researchers to address a broad range of fundamental and applied ecological questions (Caswell 2001; Morris & Doak 2002; Crone *et al.* 2011). The flexibility and power of demographic tools has increased rapidly over the last decade (Salguero-Gómez & de Kroon 2010), mirroring broad advances in computational and statistical approaches in ecology more generally (Green *et al.* 2005).

These advances have opened up new possibilities for increasing the reach of demography through quantitative

connections with diverse data sets and improved model parameterization. For example, generalized linear mixed models (GLMMs; Bolker *et al.* 2009) have been increasingly used to estimate vital rates and provide a broad platform to partition and attribute sources of variation that underlie population-level outcomes. Integral projection models (IPMs; Easterling, Ellner & Dixon 2000; Metcalf *et al.* 2013; Merow *et al.* 2014a) have allowed demographers to more comprehensively represent population structure by incorporating both continuous state variables (e.g. size [Easterling, Ellner & Dixon 2000], fur colour [Coulson *et al.* 2011]) and discrete stages (e.g. age [Childs *et al.* 2003], sex [Schindler *et al.* 2015], or developmental stage [Zambrano & Salguero-Gómez 2014]). Other recent modelling advances, such as integrated population models (Abadi *et al.* 2010) and physiologically structured models (de Roos & Persson 2001), expand opportunities by combining different data types to understand variation in vital rates. In effect, whereas many of the early population-level contributions to ecology were along theoretical lines, the new frontier emphasizes a much greater capacity for empirical connections that incorporate population structure.

How, and to what extent, can demographic approaches connect with other areas of ecology and evolution *today*? A broad literature survey using search terms aligned with different biological levels of organization points to large overlaps between populations and other scales in ecology and evolution (Fig. 2). Cutting edge research grounded in demography sits at the intersections in Fig. 2. For example, recent studies have used demography to empirically examine questions in

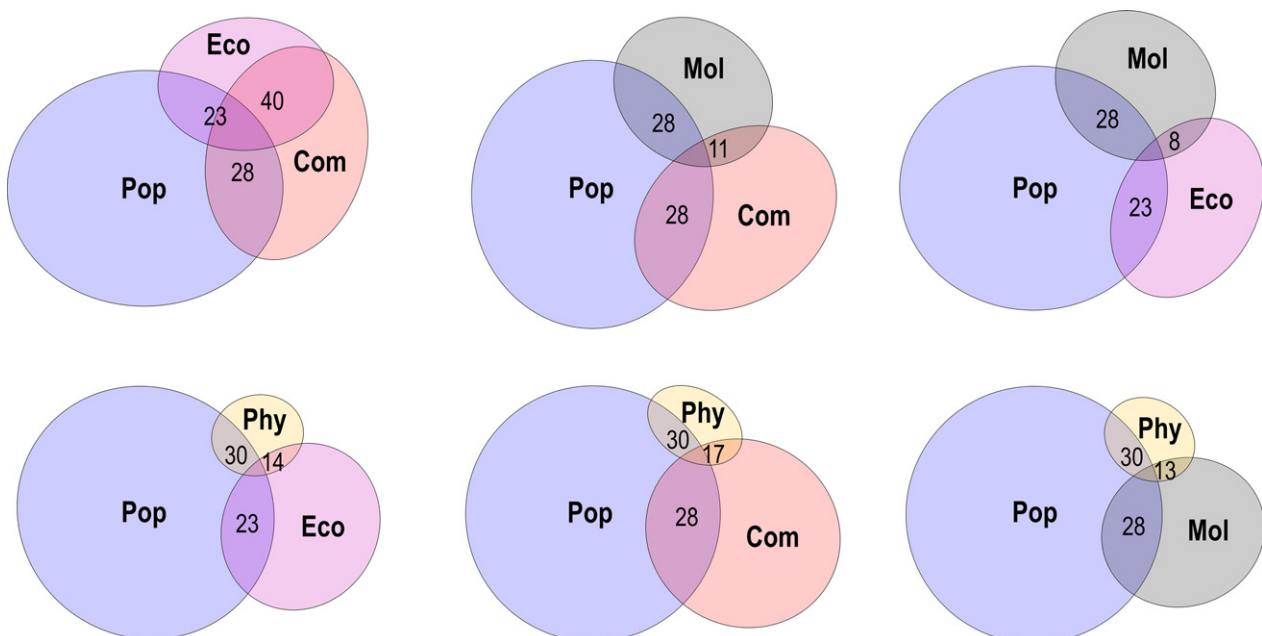


Fig. 2. Area-proportional Euler diagrams based on Web of Science search results. We searched for articles (on 29 October 2015) published since 1990 within the ‘ecology’ and ‘evolutionary biology’ categories in the Web of Science Core Collection data base (used to avoid duplicates across multiple data bases). Labels refer to topic (*ts=*) search terms: Eco = *ecosystem**, Com = *communit**, Pop = *population**, Phy = (*physiolog** or *ecophysiolog**), and Mol = (*molecul** or *chemical**). Values represent two-way intersections as a percentage of the smaller set (i.e. percentage of maximum possible size). We show only the three-way diagrams that involve the *population** search term, which also depict all other two-way intersections. Euler diagrams were created with ellipses to allow for accurate quantitative representation using eulerAPE (Version 3; Micallef & Rodgers 2014).

community ecology regarding community structure, species coexistence and niche theory (Adler, Ellner & Levine 2010; Cipriotti *et al.* 2014; Diez *et al.* 2014; Lasky *et al.* 2014). Links between physiology, functional traits and demography are increasingly being examined (de Roos & Persson 2001; Martínez-Vilalta *et al.* 2010; Zanette, Clinchy & Suraci 2014; Larson *et al.* 2015), with implications ranging from the demographic scaling of environmental drivers in species range models (Merow *et al.* 2014b; Normand *et al.* 2014) to our understanding of forest community dynamics (Iida *et al.* 2014). Molecular tools to estimate past population size and/or structure have been widely used (Roman & Palumbi 2003; Jakob *et al.* 2010), and recent work has incorporated molecular techniques to improve estimates of demographic parameters for current populations that are challenging to monitor (Meijer *et al.* 2008; Caniglia *et al.* 2014). Spanning multiple intersections, several research groups have used demography to model large-scale ecosystem processes and function (Medvigy *et al.* 2009; Vanderwel, Coomes & Purves 2013; Haverd *et al.* 2014). The 20 articles in this special feature build upon the recent research momentum within these ecological intersections and address specific challenges moving forward. Collectively, the articles: (i) explore the ways in which demography intersects with other areas of ecological and evolutionary research, (ii) identify gaps that can be informed by an understanding of population-level processes, and (iii) elucidate analytical tools and metrics that facilitate the integration of population-level processes across organizational, spatial and temporal scales.

Opportunities and challenges in the special feature

Extending the reach of demography involves both opportunities and challenges. Here, we briefly highlight the contributing articles within a broader narrative explicitly structured around these opportunities and challenges. We begin by considering the concept of the 'trait' and how it represents a key interface between biology and modelling. We argue that linking traits to their demographic consequences can provide a broad platform for addressing a range of questions. We then focus on our fundamental understanding of the drivers of demographic variation, which is critical to the broader application of demography. Several papers also address ways to improve inference given data complexity and limitations inherent in many demographic data sets. Finally, we discuss the role of demography in informing ecological applications and improving forecasting in a changing world.

THE TRAIT CONCEPT

A central focus of demography is to characterize how variation among individuals contributes to population-level performance. Individual variation is often adequately represented by traits such as size, developmental stage, age or location, *that is* the 'state variables' of structured population models. Yet, traits of interest may also be highly relevant to disciplines

such as anatomy, physiology, genetics or community ecology (Uriarte *et al.* 2016). Some traits may also pose important interacting effects by differentially influencing vital rates across ontogeny (Visser *et al.* 2016). Thus, determining how various traits affect fitness and 'scale-up' to influence other ecological processes/interactions may crucially involve structured population models that capture the complete life cycle.

With an interest in the drivers of selection on heritable traits, Rees & Ellner (2016) present a powerful approach to decompose components of natural selection in structured populations using IPMs. Unlike evolutionary models of selection that ignore population structure, they demonstrate the importance of changes in structure itself in determining selection on traits. This approach relies on an extension of structured populations (e.g. based on size) onto an additional trait axis. Similarly, Childs, Sheldon & Rees (2016) incorporate multiple structuring dimensions to examine selection on labile traits (egg-laying date in this case), which can vary throughout an individual's lifetime. Their approach captures the cumulative influence of variable environments experienced over a lifetime to improve our understanding and projections of trait evolution in wild populations.

Variation in continuous traits is also critical for understanding the complex dynamics of infectious diseases. Metcalf *et al.* (2016) present a novel use of IPMs to simultaneously capture both relevant individual differences (e.g. viral load, host susceptibility) and important population-level effects such as density-dependent transmission. These models can be nested within existing disease modelling frameworks (SIR in this case), increasing the ability to incorporate continuous traits in a flexible manner. This approach points to a promising new avenue for modelling disease dynamics and also highlights the reach of ecological methods into the realm of public health and medical research.

Trait variation is central to an important goal of functional ecology: the identification of organismal characteristics that are relatively easy to measure *in situ*, and which convey meaningful biological information (Violle *et al.* 2007). From a demographic perspective, we feel that these characteristics are too often pre-named *functional* traits without a careful consideration of their effects on fitness components. Surprisingly, the first formal test of the impact of plant functional traits on the demographic processes involving the full life cycles of plant species took place only 2 years ago (Adler *et al.* 2014). Two articles in this special feature shed light on the demographic effects of functional traits and their ecological consequences. Visser *et al.* (2016) examine how traits may differentially affect demographic rates across ontogeny. Critically, the authors find that traits often have opposing effects at different points in the life cycle, highlighting the importance of a comprehensive understanding of net effects. The influence of functional traits is scaled up to the community dynamics of a tropical forest in Costa Rica by Uriarte *et al.* (2016). They use an innovative Bayesian approach to study forest succession, linking individual tree growth and mortality to species traits, forest structure and climatic variation. Taken together, these studies suggest that the prospect

of demographically based forecasts derived from traits may be on the horizon, even for species with few direct demographic observations (e.g. [Merow *et al.* 2014b](#)).

UNDERSTANDING VARIATION AND THE DRIVERS OF POPULATIONS

In order to link demographic processes with other research areas in ecology and evolution, it is crucial that we continue to expand our understanding of the underlying factors that govern population dynamics. In addition to the examples highlighted above, linking traits and demography also provide an opportunity to better understand the sources of demographic variation. To this end, [Plard *et al.* \(2016\)](#) decompose the population growth rate to show how it is affected by changes in trait means and variances. The authors find that population dynamics may be more sensitive to changes in the *curvature* of the relationship between traits and vital rates (as opposed to the overall strength) and that phenotypic variation may be more consequential for populations of short- vs. long-lived species.

Other key sources of demographic variation have often been overlooked or considered as ‘noise’. For example, although there has been a great deal of work on the nature and effects of stochastic temporal variation on populations (e.g. [Fieberg & Ellner 2001](#); [Doak *et al.* 2005](#); [Boyce, Haridas & Lee 2006](#); [Metcalf *et al.* 2015](#)), much less attention has been paid to the contributions of fine-scale spatial heterogeneity on population dynamics (but see [Rebke *et al.* 2010](#)). Using a long-term data set of a perennial plant, [Crone \(2016\)](#) finds that increased spatial heterogeneity across a relatively small area (< 0.25 ha) promotes the population growth rate, distinctly contrasting with the negative effect of temporal variation. Such opposing effects of two ubiquitous sources of variation may have important consequences for both applied forecasting and basic ecology research, as space-for-time substitutions are frequently carried out in field ecology ([Merow *et al.* 2014b](#); but see [Tielbörger & Salguero-Gómez 2014](#)). In a similar vein, [McDonald *et al.* \(2016\)](#) explore the role of transient (short term, non-stationary) dynamics on structured population growth rates. Although transient dynamics are common in natural systems ([Maron, Horvitz & Williams 2010](#); [Stott, Townley & Hodgson 2011](#)), demographic research has mostly focused on asymptotic metrics ([Hastings 2004](#); but see [Williams *et al.* 2011](#)). [McDonald *et al.*](#) use an extensive comparative demography approach with over 130 plant species from the COMPADRE Plant Matrix Database ([Salguero-Gómez *et al.* 2015b](#)) and find the contribution of transient dynamics to stochastic growth rates to be equally as large on average compared to asymptotic (long term, stationary) contributions. Together, these papers emphasize the need for a more comprehensive understanding of the underlying spatial and temporal components of population dynamics.

The influence of abiotic and biotic environmental factors (climate, resources, disturbance, predators, etc.) on vital rates and resulting population dynamics represents another critical source of variation that is often not explicitly accounted for in

demographic studies ([Crone *et al.* 2013](#)). Moreover, these factors embody the underlying ecological drivers of populations and thus represent critical mechanisms for scaling and projections. In a comprehensive review of research on environmental drivers in structured population models for over 130 plant species, [Ehrlén *et al.* \(2016\)](#) find that such studies are indeed on the rise. However, they point to several gaps in the literature that beg for further research, such as density-dependent interactions, dynamic feedbacks, trait evolution and the incorporation of drivers as continuous metrics. With this insight, the authors provide recommendations to inform the design of studies aimed at addressing these gaps. [Treurnicht *et al.* \(2016\)](#) make progress in several of these areas with an extensive examination of how abiotic factors and intraspecific density relate to the fecundity and recruitment rates of 26 shrub species from South Africa. Across entire species’ ranges, climate and fire emerge as dominant drivers, but with effects at distinctly different parts of the life cycle, similar to the results found by [Visser *et al.* \(2016\)](#).

Environmental conditions may also be inferred by trait values themselves ([Beckerman *et al.* 2003](#)). Using a novel regression-based variance decomposition approach, [Brooks *et al.* \(2016\)](#) investigate how the body size of soil mites can act as a proxy for past environments. They show that prior food availability has differential effects on distinct vital rates, including how these influences are mediated through the more proximate effect of body size. [Henning-Lucass *et al.* \(2016\)](#) indirectly examine past environments using a resurrection ecology approach and compare *Daphnia* populations, dormant for four decades, to current populations from the same lake. They find strong plasticity to water temperature for past and current populations (with important effects on key vital rates) as well as some evidence for recent microevolution in this plastic response.

The overarching issue of correctly identifying the influence of one or more particular environmental factors is addressed by [Teller *et al.* \(2016\)](#). In practice, researchers often rely on arbitrary decisions about the spatial scale over which competition occurs and aggregate continuous climate data into discrete lags representing factors such as mean temperature. These aggregations are often chosen *a priori* and could easily average over important variability. Given enough data, [Teller *et al.*](#) show how spline methods can help avoid such *a priori* decisions. At larger spatial scales, different factors may emerge as important drivers of metapopulation and source-sink dynamics. [Heinrichs, Lawler & Schumaker \(2016\)](#) examined over 130 different model scenarios and found that characteristics of both populations (e.g. capacity for rapid growth) and the landscape (e.g. distribution of habitat quality) contributed strongly to the emergence of source-sink dynamics. However, similar outcomes sometimes resulted across a range of different parameter values, suggesting complex interactions and scaling pathways.

CHALLENGES OF DATA LIMITATION AND UNCERTAINTY

Demography can be a ‘data hungry’ discipline. Ideally, individual transitions and reproductive rates throughout the life

cycle should be carefully detailed, but challenges can emerge from spatiotemporal coverage, imperfect observations and rare demographic events. Several manuscripts in this special feature (Kerr *et al.* 2016; McDonald *et al.* 2016) take advantage of the recent push for broad, comparative demographic analyses (Salguero-Gómez *et al.* 2015b, 2016) to address questions in ecology, evolution and conservation biology at a global level. Several calls for longer term ecological data have been made to the research community and funding agencies (Crone *et al.* 2011). The need within demography is critical, particularly for long-lived species that may encounter rare, but extremely important events such as extreme droughts, episodic fire or disease outbreaks (Needham *et al.* 2016).

An important challenge is how to incorporate key demographic rates that occur infrequently (e.g. large tree mortality and masting events) and/or are difficult to detect (true vs. apparent survival in mobile organisms, hibernation/dormancy, etc.). Barthold *et al.* (2016) directly address the latter by developing a method to estimate lion mortality that incorporates sex-biased dispersal. Until now, nomadic male lions that disperse away from prides have made it difficult to assess a critical vital rate for this declining species: male survival. Data limitations become even more apparent when extending population models to larger fields of inference, whether spatial extent (e.g. Merow *et al.* 2014b) or community complexity (e.g. Needham *et al.* 2016; Uriarte *et al.* 2016). To address this challenge, González, Martorell & Bolker (2016) use inverse models (Hartig *et al.* 2012), a promising approach to parameter estimation. With data on population abundances over time, but with incomplete information on vital rates, they are able to recover key demographic parameters. Needham *et al.* (2016) similarly use inverse models to estimate fecundity parameters of multiple species from a short-term data set. With this approach, they were able to build individual-based models (IBMs; Grimm & Railsback 2005) to examine the spatially explicit response of a forest community to a tree pathogen. Collectively, these three studies advance our ability to fill in 'holes' in demographic data sets, extending their general applicability.

ECOLOGICAL FORECASTING AND APPLICATIONS

Applied ecology has important intersections with a range of social factors (stakeholders, policy frameworks, etc.), and consequently faces more dimensions and scaling axes than are depicted in Fig. 1. For example, whereas demographic models have long been used to inform specific management action for ecosystems of species of concern (Silvertown, Franco & Menges 1996; Morris & Doak 2002; Crone *et al.* 2011), most models are based on factors that directly relate to biology and rarely explicitly incorporate other management considerations such as efficacy and cost (Shea *et al.* 2010; but see Baxter *et al.* 2006). Kerr *et al.* (2016) provide a broad evaluation of how demographic models align with other metrics relevant to cost-effective management. Indeed, they expand the boundaries of demography by linking model outputs (e.g. elasticities of population growth rate) for multiple

species to survey results of land manager action priorities. A key finding is that, while managers do incorporate demography, they face a much greater range of factors (e.g. off-target effects, social impacts) that should be more explicitly considered by ecologists as well.

Ecological forecasting has become imperative for policy and management, even as the complex dynamics of global change simultaneously increase the challenge (Mouquet *et al.* 2015). Crone *et al.* (2013) demonstrated the shortcomings of matrix population models in accurately forecasting population dynamics and suggest that a typical disconnect from environmental drivers is an important underlying factor. Promising research addressing this priority is reviewed by Ehrlén *et al.* (2016), and Treurnicht *et al.* (2016) point to the potential of environmental drivers of vital rates to inform forecasts in both space and time (e.g. range dynamics; Merow *et al.* 2014b; Normand *et al.* 2014). Wittmann *et al.* (2016) take a different angle and find that habitat suitability based on temperature for *Ctenopharyngodon idella* (grass carp) correlates with observations of individual growth rates across six continents. Their study is among only a handful that has ground-truthed the link between trait values (also a key vital rate in this case) and habitat suitability predicted using presence/absence of data.

Another potential limitation to accurate forecasting is the context of the community in which populations exist. Needham *et al.* (2016) take a step towards improving species-level forecasts by simultaneously modelling multiple members of a forest tree community. This approach enables one to incorporate constraints on limiting resources and model species interactions, which can be key to determining long-term outcomes. Uriarte *et al.* (2016) take a different approach to forecasting community dynamics by linking variation in demographic rates across multiple species to more readily observed functional traits.

As projections become a more common tool to forecast the response of natural systems to global change, computationally efficient platforms for simulations become more important (Visser *et al.* 2015). Forest simulators have a long history in the ecological literature, but few incorporate size-structure and functional traits in explicit models of plant performance and density-dependent growth. Falster, FitzJohn & Westoby (2016) introduce *plant*, an R package that simulates forest development through efficient models of populations, communities and even meta-communities. Stands can be simulated stochastically or deterministically and be used to explore a variety of eco-evolutionary questions.

Projecting forward

The 20 articles of this special feature highlight the opportunities at the intersections between demography and other disciplines. The ultimate reach of demography will depend in part on research priorities and design, and it will be increasingly important for studies to *quantitatively* leverage each other. Recent advances in comparative demography (e.g. Jones *et al.* 2014; Salguero-Gómez *et al.* 2015a) have demonstrated the

Table 1. Select software packages relevant to demographic modelling and analyses. All are open-access R packages unless otherwise noted. Descriptions are those of the package authors

Package	Description	Reference
<i>addhazard</i>	Fit additive hazards models for survival analysis	Hu, Breslow & Chan (2015)
<i>AlleleRetain</i>	Allele retention, inbreeding, and demography	Weiser (2013)
<i>BaSTA</i>	Age-specific survival analysis from incomplete capture–recapture/recovery data	Colchero, Jones & Rebke (2015)
<i>bayesSurv</i>	Bayesian survival regression with flexible error and random effects distributions	Komárek (2015)
<i>demoniche</i>	Simulating spatially explicit population dynamics	Nenzén <i>et al.</i> (2012)
<i>discSurv</i>	Discrete time survival analysis	Welchowski & Schmid (2015)
<i>dynsurv</i>	Dynamic models for survival data	Wang, Yan & Chen (2014)
<i>IPMpack</i>	Builds and analyses Integral Projection Models (IPMs)	Metcalfe <i>et al.</i> (2013)
<i>lme4</i>	Linear mixed-effects models using ‘Eigen’ and S4	Bates <i>et al.</i> (2015)
<i>loop</i>	Loop decomposition of weighted directed graphs for life cycle analysis, providing flexible network plotting methods and analysing food chain properties in ecology	Chen (2012)
<i>marked</i>	Mark-recapture analysis for survival and abundance estimation	Laake, Johnson & Conn (2015)
<i>MCMCglmm</i>	MCMC generalized linear mixed models	Hadfield (2015)
<i>NEff</i>	Calculating effective sizes based on known demographic parameters of a population	Grimm & Henle (2015)
<i>plant</i>	A package for modelling forest trait ecology & evolution	Falster, FitzJohn & Westoby (2016)
<i>popbio</i>	Construction and analysis of matrix population models	Stubben, Milligan & Nantel (2015)
<i>popdemo</i>	Provides tools for demographic modelling using projection matrices	Stott, Hodgson & Townley (2014)
<i>popEpi</i>	Functions for epidemiological analysis using population data	Miettinen <i>et al.</i> (2015)
<i>PSPManalysis*</i>	Physiologically structured population models	de Roos (2015)
<i>PVAClone</i>	Population viability analysis with data Cloning	Nadeem & Solymos (2014)
<i>Rramas</i>	Matrix population models	de la Cruz (2014)
<i>spatialdemography</i>	Spatially explicit metacommunity model	Keyel, Gerstenlauer & Wiegand (2015)
<i>stagePop</i>	Modelling the population dynamics of a stage-structured species in continuous time	Kettle (2015)
<i>survival</i>	Survival analysis	Therneau & Lumley (2015)

*PSPManalysis is implemented in C with R and MATLAB front-ends.

potential of this approach. Yet, most demographic studies are highly variable in nature and implementation and not designed with the foresight to connect with other data sets and extend beyond the original study goals. With emergent open-access demographic data repositories (Lebreton *et al.* 2010; Salguero-Gómez *et al.* 2015b, 2016) and a greater capacity to quantitatively integrate data sources, demographers should consider how to maximize the broader potential of their data when designing studies. For example, while collecting demographic data, researchers may want to consider certain covariates that are broadly informative (e.g. density, environmental factors), and which are relatively easy to measure (Ehrlén *et al.* 2016). In this sense, one might extend the concept of comparative demography to that of *collective* demography, where demographic data are collected with the *a priori* consideration that they can inform a broader suite of ecological and evolutionary questions. This is similar to the software engineering concept of *extensibility*, where future use and compatibility are explicitly considered in the process of designing a flexible system (Erdogmus & Tanir 2002).

Beyond the requirements of the data themselves, demographic advances have relied on developing novel quantitative tools. Luckily, the last decades have witnessed unprecedented progress in open-access software packages that allow users to implement modelling techniques in a relatively straightforward manner (see software packages in Table 1). In addition,

many of the manuscripts in this special feature have provided open-access R scripts of their analyses in their online materials (e.g. Childs, Sheldon & Rees 2016; Teller *et al.* 2016).

To mark the 100th anniversary of the BES, Sutherland *et al.* (2013) formulated a list of 100 standing questions in ecology and evolution. We were struck by the degree to which demography and population-level processes are relevant to these questions. Naturally, we have no doubt that other approaches also have considerable and complementary reach, and we emphasize that our focus on demography is not mutually exclusive vis-a-vis other disciplines. What we see is an emerging opportunity, illuminated by a recent surge in diverse demographic research avenues and connections. There is much to be gained by harnessing and directing this momentum towards greater ecological consilience.

Acknowledgements

We are grateful to the British Ecological Society for their support during the organization of the symposium ‘Demography Beyond the Population’ (especially to A. Simpson, A. Everard and R. English), and the special feature (especially to A. Baier and L. Sandhu). Many thanks are also due to the over 40 anonymous referees involved in this special feature. J. Vaupel provided useful comments on earlier drafts of this manuscript. A.B.G. was supported by Wellesley College. R.S.G. was supported by the Australian Research Council (DE140100505) and by the Max Planck Institute for Demographic Research. C.M. was supported by USDA-NRI 2008-35615-19014 and NSF CHN 1414108. C.M. and S.M. were supported by NSF DEB-1137366.

Data accessibility

This paper does not use data.

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Received 20 November 2015; accepted 20 January 2016

Handling Editor: David Gibson