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What's hot in conservation biogeography in a changing climate? Going beyond species range dynamics

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1 | INTRODUCTION

In recent decades Earth's rapidly changing climate, driven by anthropogenic greenhouse gas emissions, has affected species distributions and phenology, ecological communities and ecosystem processes, effects that are increasingly being observed globally (Allen et al., 2010; Doney et al., 2012; Franklin, Serra-Diaz, Syphard, & Regan, 2016; Parmesan, 2006; Walther et al., 2002). Pleistocene shifts in species ranges during glacial–interglacial transitions reveal large-scale biome shifts and non-analog species assemblages (MacDonald et al., 2008; Nolan et al., 2018; Williams & Jackson, 2007); the pace of current anthropogenic warming outstrips past changes in the Earth system and climate, however, leading to new climate novelties and ecological communities (Ordonez, Williams, & Svenning, 2016). Global scientific consensus now emphasizes that global warming should be kept to 1.5°C to avoid catastrophic changes in ecosystems and the services they provide to people (IPCC, 2018), and climate change threats to biodiversity are being prioritized in international policy response (Ferrier et al., 2016).

Conservation biogeography addresses the impacts of global change on the distribution of species, communities and ecosystems with implications for large-scale conservation assessment and planning (Franklin, 2016; Richardson & Whittaker, 2010). Species distribution models—statistical models associating the spatial distribution of species with climate and other environmental factors (Franklin, 2010a)—have been used to project the impacts of climate change for large numbers of species, across taxonomic groups, at large spatial scales. Furthermore, they have been used to assess protected area network effectiveness under a fast warming climate (Araújo,

Alagador, Cabeza, Nogués-Bravo, & Thuiller, 2011). Models based on spatial-statistical correlation are a “first approximation” of species' *exposure* risk to climate change—the magnitude of change in conditions experienced by a species sensu Dawson, Jackson, House, Prentice, & Mace (2011)—but even such magnitude of change can be misleading to prioritize conservation efforts (Sofaer, Jarnevich, & Flather, 2018).

There have been calls for a more comprehensive approach to risk assessment and projections (Franklin, 2010b; Guisan & Thuiller, 2005), and consequently, other data and methodologies are increasingly being brought to bear on this important problem, including disturbance and management scenarios in range change projections (Serra-Diaz, Scheller, Syphard, & Franklin, 2015), accounting for realistic dispersal (Aben et al., 2016; Bocedi et al., 2014; Engler, Hordijk, & Guisan, 2012) and incorporating important processes not explicitly addressed in SDMs such as biotic interactions (Hof, Jansson, & Nilsson, 2012), the adaptive capacity of organisms (Bush et al., 2016) or more generally eco-evolutionary dynamics (Legrand et al., 2017). In summary, there is a clear need to improve our forecasting capacity of climate change (Urban et al., 2016).

In the context of the persistent lack of widespread biodiversity data, with shortfalls ranging from species discoveries, lack of known ranges and shortage of abundance data (Hortal et al., 2015), it is not surprising that SDMs are still a dominant tool in conservation biogeography, but we argue that their use under climate change needs to explore further dimensions of conservation biogeography, beyond range change projections. The group of papers featured in this Special Issue portray a wide range of different approaches to study climate change from a conservation biogeography perspective. They

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explore key aspects of climate change and conservation, both detecting climate change-driven biodiversity change in key biogeographical hotspots, and projecting climate change impacts in the future in ways that move beyond static, range-wide, single-species approaches. These projections incorporate biotic interactions, community models, physiologically constrained models and experimental data. They disentangle the effects of multiple global change drivers and inform conservation policy and management. We highlight key findings from the Special Issue, grouped by these themes, in the following sections.

2 | DETECTION-ATTRIBUTION MATTERS FOR CONSERVATION BIOGEOGRAPHY

Ongoing monitoring and reporting of current biodiversity shifts in biodiversity hotspots is needed, as sensitivity and adaptive capacity of species could offset the exposure to climate change predicted by species distribution models (Dawson et al., 2011). The first group of papers uses multiple lines of evidence to detect biodiversity change attributable to climate change within bird (Flesch, 2019) and moth (Cheng et al., 2019) communities, highlighting the value of long-term monitoring. Flesch (2019) detected changes in bird communities in isolated mountain ranges in arid northern Mexico using extensive historical and modern survey data and was able to attribute community change to climate, land use and landscape configuration—changes that depended on species traits. Cheng et al. (2019) used 15 years of monitoring data for geometrid moths in a lowland tropical ecosystem (Hong Kong) with Bayesian occupancy modelling, detecting an upward elevation shift in the moth community consistent with changes in temperature, but possibly also influenced by indirect climate effects on biotic interactions (distributions of host plants and avian predators).

At the species level, dedicated sampling along longitudinal sites can help determine species' early warning signs of decline. In this issue, Matías, Abdelaziz, Godoy, and Gómez-Aparicio (2019) shows how different biotic and abiotic factors can shift within the tree species *Quercus suber*—an economically important tree species in the Iberian Peninsula. Understanding such demography variations to detect within-species' decline may better help connect conservation biogeography with local management applications. Additionally, these authors found not only climate but also pathogen abundance to determine the demographic structure the species. In a more connected world, such new pathogens may increase their importance and will be crucial to determining conservation potential (Millar & Stephenson, 2015; Roy et al., 2017).

3 | PROJECTING SPECIES DISTRIBUTION AND ABUNDANCE BEYOND SINGLE SDM RANGE SHIFTS

Three papers explore different ways of projecting climate change on species distributions to inform conservation biogeography, beyond

projecting suitability-derived SDM outputs for species. Braz, Lorini, and Vale (2019) propose a method for distribution modelling of parapatric species, combining SDMs and niche overlap analysis to determine biotic and abiotic components of parapatry. They found that climate change may affect distribution but not parapatry of Brazilian marmoset monkeys. Incorporating ad hoc biotic interactions via niche equivalency analysis may be a promising way to project climate changes and biotic interactions for numerous species, where other approaches would be limited by computational constraints.

Caddy-Retalic et al. (2019) applied community composition approaches to analyse plant and ant assemblages in South Australia based on ordination techniques. Projections under climate change highlighted a higher sensitivity of ant versus plant assemblages and a substantial decoupling of these communities under climate change. Benedetti, Ayata, Irisson, Adloff, and Guilhaumon (2019) explored the interface between traditional species-centred conservation biogeography and functional biogeography. They compared whether potential shifts in species richness in copepods under climate change equated to shifts in functional diversity and found that sensitive species were functionally redundant.

As part of a long-standing call for mechanistically informed understanding and prediction of species distributions, two papers in this issue explore physiological constraints for climate change projections. Wilson, Skinner, and Lotze (2019) compared physiological and correlative species distribution models for intertidal organisms. They found that projections of SDMs agreed with physiologically informed thresholds. Casties, Clemmesen, and Briski (2019) used a common-garden experiment analysing temperature and salinity to get at gammarid species tolerances in order to assess potential invasion success in the Baltic sea.

Temporal dynamics affect population trends, identify corridors and project range shifts. This may have a strong bearing on the temporal scale at which species vulnerability plays out during the 21st century (e.g., mid vs. end of the century differences, Serra-Diaz et al., 2014). Incorporating the effects of interannual variability and extreme events are important for predicting current species ranges (Early & Sax, 2011; Zimmermann et al., 2009), but to what extent these effects on species abundances persist, and whether correlative models are able to predict these effects are still subject to further scrutiny. Two studies in this Special Issue shed light on these key questions. Maxwell et al. (2019) reviewed 519 studies and reported 60% in which extreme weather events influenced population dynamics for more than one year, and in 38% of the studies species and ecosystems showed no recovery from previous extreme-event conditions. In another study, Becker et al. (2019) showed that models built using data collected over multiple decades are able to forecast abundance and distribution of cetacean species in the California Current ecosystems for a novel extremely warm year of 2014.

Two papers illustrate how important it is to consider multiple global change drivers spatially when forecasting future scenarios for conservation biogeography—namely the interactions of climate change and land-use change (e.g., Conlisk et al., 2013; Franklin, Regan, & Syphard, 2014). The case study by Di Febbraro et al. (2019), using circuit theory

methods to address range connectivity, shows that while four alien squirrel species introduced in Europe are projected to expand their ranges under climate change, a reduction in invasion risk is projected when land-use change projections are also considered as a result of loss of suitable habitat and dispersal corridors. In their study of over 1,500 plant species in the South American Cerrado, Velazco, Villalobos, Galvão, and De Marco Júnior (2019) were able to project where the separate and combined effects of climate and land-use change are most likely to affect this biome by the end of the century.

4 | OUTPUTS EXPLORING POLICY, MANAGEMENT AND PLANNING

Models of species distributions have been used extensively to assess the effectiveness of conservation areas. Climate change is expected to cause significant shifts in biogeographical barriers and movement of species. Beyond elevation shifts in mountain ranges, there is mounting evidence that melting of Arctic sea ice will cause dramatic exchanges in birds and mammals (McKeon et al., 2016), and fish interchanges (Wisz et al., 2015). This is likely to shape communities and hence conservation prioritization and conservation planning in a rapidly warming climate.

Projections of such climate change caused redistribution and the new assemblages arising from it may redefine protected area corridor networks. Coarse-filter (Carroll, Parks, Dobrowski, & Roberts, 2018) and fine-filter approaches (Lawler, Ruesch, Olden, & McRae, 2013) have been used to assess current and potential future species redistributions, but how these corridors and shifting species' ranges translate into conservation strategies needs to take into account political entities. Montesino Pouzols et al. (2014) showed, in a global protected area analysis, how noncoordinated efforts in spatial conservation planning (national level) would at best cover 70% of the species and ecoregions protected if an international coordinated effort would be in place. In this issue, Thornton and Branch (2019) performed range analysis across countries in different geographical directions and compared that to the asymmetries in country-level conservation status. They analysed conservation listing of transboundary mammals in the Americas, and found that for 850 species with poleward transnational range limits, 26% had different conservation status among countries. Velazco et al. (2019) showcased the importance of coordinated transboundary efforts for Cerrado biodiversity. In their projections of 1,553 plant species, they found a future potential loss within the protected areas of Bolivia, Brazil and Paraguay, underscoring the inadequacy of the current network of protected areas in a rapidly changing world.

5 | NEW OPPORTUNITIES FOR CLIMATE CHANGE RESEARCH IN CONSERVATION BIOGEOGRAPHY

In summary, following calls to move beyond static species distribution modelling in order to forecast global change threats to global

biodiversity (Franklin, 2010b; Guisan & Thuiller, 2005; Urban et al., 2016), researchers, including those featured in the Special Issue, have worked to fill the gap, applying new methods, data and experiments.

Detection of range shifts and attribution to climate change remains a critical challenge and this important objective relies on carefully curated long-term data or historical surveys (e.g., Freeman, Scholer, Ruiz-Gutierrez, & Fitzpatrick, 2018; Kuhn & Gégout, 2019; Yalcin & Leroux, 2018). Data documenting observed changes are being aggregated into big data compilations (e.g., biodiversity time series (Dornelas et al., 2018)), and information is being improved to better inform conservation prioritization. Country species checklists are starting to gain momentum due to more institutional collaboration around the world. Examples are recently published tree species lists or large-scale aggregation of occurrence data either by institutions (e.g., GBIF <http://www.gbif.org> or Atlas of Living Australia <http://www.ala.org.au/> among others, the list could be long) or by research teams (e.g., DRYFLOR, <http://www.dryflor.info/>; Serra-Diaz, Enquist, Maitner, Merow, & Svenning, 2017), world checklists (<http://www.theplantlist.org/>), or the well-known world protected area databases (<https://www.protectedplanet.net/c/world-database-on-protected-areas>). This growing world of data infrastructure nonetheless requires improvements and maintenance over time. Thus, data generation and curation in conservation biogeography—data science—needs further development in conservation biogeography including standardized protocols for models, data version controls and procedures for, for example, occurrence data cleaning and quality assessment (Franklin, Serra-Diaz, Syphard, & Regan, 2017 and references therein).

New approaches in conservation biogeography are still needed to forecast range shifts, and resulting conservation and restoration decisions. New methods that can address biodiversity response to global change at the community level include joint species distributions models (Pollock et al., 2014) that can generate projections for a large number of species. A coupled modelling approach has been used to inform traditional niche models with regard to population processes (Franklin et al., 2014; Zurell et al., 2016). New tools for incorporating demographic effects directly into projected range dynamics are being developed (e.g., Evans, Merow, Record, McMahon, & Enquist, 2016; Merow et al., 2014; Pironon et al., 2018). Furthermore, simulation models can dynamically account for the synergistic effects of climate change and land-use change or disturbances (Bocedi et al., 2014; Boulangeat et al., 2014). Species composition may swiftly change after a disturbance event and humans play a key role in shaping disturbance regimes (Syphard et al., 2007) with consequences for species conservation (Regan et al., 2012). The overall effect of disturbances, however, still requires further scrutiny. For instance, Liang, Duvenceck, Gustafson, Serra-Diaz, and Thompson (2018) predicted little effect of disturbances on range edge shifts in NE United States forests while Serra-Diaz et al. (2018) projected rapid conifer decline due to climate–fire interactions in western United State forests. Finally, niche and network approaches could be important for predicting ensembles of species under climate change (Godoy, Bartomeus, Rohr, & Saavedra, 2018), providing new avenues for research in conservation biogeography.

Experiments have not been used extensively in conservation biogeography in a changing climate albeit have proven to be informative. Considering intraspecific variation may be key to assessing real extinction outcomes from climate change (Benito Garzón, Alía, Robson, & Zavala, 2011). For instance, trait-based models of tree performance based on experiments (provenance trials) resulted in robust forecasts of climate change impacts on a species under nonanalog conditions (Chakraborty, Schueler, Lexer, & Wang, 2019). Trait-based approaches are increasingly being used as a lens for viewing the dynamics of ecological communities in a mechanistic way (Violle, Reich, Pacala, Enquist, & Kattge, 2014), including under climate change (e.g., Anderegg, 2015; Santini et al., 2016; Sunday et al., 2015). Model inter-comparison (e.g., mechanistic vs. correlative) may help disentangle biotic versus abiotic constraints (Keenan, Serra-Diaz, Lloret, Ninyerola, & Sabate, 2011) and could be combined to produce better ecological forecasting (Talluto et al., 2016). All in all, these new models and modelling approaches provide a way forward for projecting climate change opportunities and vulnerabilities in a context of rapid climate shifts and extinction rates, where models assuming equilibrium of species distributions with climate may not provide suitable answers for short-term (e.g., 20–30 years) dynamics.

Understanding the spatial context in which conservation takes place may benefit from further developments (Ackerly et al., 2010). In the last decade, several indices have been developed to understand and prioritize regions of rapid biodiversity change. Metrics like climate velocity (Burrows et al., 2014; Loarie et al., 2009), biotic velocities (Carroll, Lawler, Roberts, & Hamann, 2015), bioclimatic velocities (Serra-Diaz et al., 2014) or novel climates (Ordóñez et al., 2016), and comparison among those (Comte & Grenouillet, 2015), are used to integrate spatial and temporal dimensions of climate change for one or several species. Developing new methods and metrics that easily capture dimensions of range shifts important to conservation is still a priority. For instance, Dobrowski and Parks (2016) pointed out that existing metrics may underestimate vulnerability in some regions because they do not account for dispersal routes. Additionally, given the availability of new high-resolution climate products and methods for microclimate estimation (Kearney & Porter, 2017), identifying migration routes and (micro)refugia under climate change may now be possible (Dobrowski, 2011). Spatial prediction of these small-scale opportunities for conservation is also a research opportunity for conservation biogeography, as they could buffer climate change effects on biodiversity loss, and can affect spatial conservation planning (Hannah et al., 2014; Keppel et al., 2015; Lenoir, Hattab, & Pierre, 2017). Likewise, it has been acknowledged that vegetation structure—notably canopy cover—could also reduce the impact of climate change as canopies tend to reduce the realized temperature of organisms understory (Frey et al., 2016), and accounting for this in distribution models has been proposed (Lembrechts, Nijs, & Lenoir, 2018).

New avenues of research are needed to guide ecosystem management, inform conservation policy and design nature-based solutions to global change. Proposed mitigation measures to

reduce net carbon emissions and offset global warming, such as crop biofuels and solar geoengineering themselves may have consequences for ecosystems processes and species range dynamics, recently also addressed through model-based forecasting (Dagon & Schrag, 2019; Hof et al., 2018; Trisos et al., 2018). Similarly, new approaches of nature-based solutions to biodiversity conservation consider interesting strategies such as trophic rewilding—the re-introduction of species to promote self-regulation of biodiverse ecosystems (Svenning et al., 2016). However, how widely these new strategies can actually be implemented under future climate change should be further explored. A recent example Jarvie and Svenning (2018) showed that trophic rewilding is a viable approach under climate change, as 17-large-bodied candidates for trophic rewilding would be retained under different climate change scenarios.

Conservation biogeography under climate change has benefited largely from our capacity to project in space and time distribution of taxa. As new data, methods and conservation approaches arise, widening the horizons of the field implies pushing the limits of what now have become models with developed standards (Araújo et al., 2019), and consider how other less-used techniques such as experiments and biophysical model or ecological network approaches can better inform conservation over space and time. Grounding our research questions to respond to policy and management needs will be key to continue making conservation biogeography a transformative field in the Anthropocene.

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