Connectivity for species on the move: supporting climate-driven range shifts

Caitlin E Littlefield^{1*}, Meade Krosby², Julia L Michalak¹, and Joshua J Lawler¹

Many species are already responding to global climate change by shifting their ranges to track suitable climatic conditions. However, habitat loss and fragmentation, coupled with the rapidity of climate change, make it difficult for species to keep pace. It is therefore unsurprising that enhancing landscape connectivity is the most frequently cited climate-adaptation strategy for conserving biodiversity. Yet most connectivity planning, even if intended to address climate change, does not directly take climate change and climate-driven range shifts into account. Nonetheless, several approaches that do explicitly address the unique challenges posed by climate change have recently emerged. We review these connectivity modeling approaches: specifically, how they incorporate species' responses, identify movement routes, and address uncertainties. Despite this proliferation of approaches, conceptual and analytical hurdles remain, and meeting these challenges will be critical to achieving effective landscape connectivity for species in the face of climate change.

Front Ecol Environ 2019; 17(5): 270-278, doi:10.1002/fee.2043

Geographic range shifts have been vital to species' persistence during past periods of global climate change (Davis and Shaw 2001). In response to current global warming, many species have already shifted range boundaries to track suitable climatic conditions (Parmesan and Yohe 2003). However, the rapid pace of modern climatic changes, coupled with habitat loss and fragmentation, are making it difficult for species to follow preferred climatic conditions and call into question the effectiveness of this adaptive response (McGuire *et al.* 2016).

In a nutshell:

- Increasing landscape connectivity is one of the most frequently recommended adaptations for conserving biodiversity as the global climate changes
- However, few existing connectivity modeling approaches directly account for climate change
- Emerging methods to directly address climate-driven movements generally rely on projected range shifts, climate trajectories and analogs (ie historical and future conditions that match), existing climatic gradients, and geophysical settings
- Despite advances in this modeling realm, hurdles still remain – for example, addressing the spatial and temporal dynamism of climatic changes, capturing elusive climatic refugia, and managing uncertainties in species' responses
- In addition to addressing these challenges, connectivity models and plans will need to be tested

 ¹School of Environmental and Forest Sciences, College of the Environment, University of Washington, Seattle, WA *(caitlin.littlefield@umontana.edu);
 ²Climate Impacts Group, College of the Environment, University of Washington, Seattle, WA For this reason, enhancing landscape connectivity – the degree to which the structure of the landscape facilitates species' movement – is the most frequently cited climate adaptation strategy for biodiversity conservation (Heller and Zavaleta 2009). Landscape connectivity has already been incorporated into many climate adaptation planning efforts at regional, national, and international scales (eg WGA 2008; NPS 2010; Natura 2000 Network, https://bit.ly/1i2vgXI), but most connectivity planning does not directly take climate change into account (Mazaris *et al.* 2013). That is, the bulk of studies and planning efforts that claim to use connectivity among existing habitat patches rather than explicitly addressing the unique needs presented by climate-induced range shifts (Table 1).

To some extent, enhancing connectivity based on current habitat location and quality will increase the capacity of species to move in response to climate change simply because such efforts should increase the permeability of the landscape in general. However, preliminary comparisons suggest that this will not always be the case (Littlefield et al. 2017). Changes in climatic conditions will, in many cases, shift the location and availability of suitable habitat, necessitating directional movements from current to future areas of climatic and habitat suitability (Krosby et al. 2010). Accounting for these shifts requires that models identify not only where high-quality habitat is currently located but also where it will be in the future. In addition to modifying the distribution of core habitat, climate change may constrain or alter the viability of movement routes needed to make newly suitable habitat accessible. Finally, climate-driven range shifts may lead species into habitat "culde-sacs", such as the tops of mountains (Carroll et al. 2015).

A wide range of approaches for explicitly addressing these unique challenges posed by climate change has emerged in recent years. These approaches vary in their complexity and Table 1. A comparison of objectives, targets, inputs, and potential sources of uncertainty in models and plans for traditional connectivity and those for connectivity specifically designed to address species' responses to climate change

		Modeling approach	
Category	Feature	Traditional	Climate-driven
Primary conservation objective	Maintain or restore movement among fragmented habitats	V	
	Promote climate-driven shifts in species' ranges		v
Potential model focus or what is being connected	Protected areas	 	
	Natural landscapes	v	
	Geophysically diverse areas	v	~
	Current ranges or habitat	v	~
	Future ranges		~
	Current and future climate conditions		V
	Climate gradients (eg warm to cool)		v
Potential model inputs	Land cover or landscape resistance	v	v
	Geophysical features	~	~
	Habitat suitability models	v	~
	Current climate	~	~
	Future climate		~
	Species distribution models		~
Sources of uncertainty	Landscape resistance	v	~
	Geophysical datasets	~	~
	Habitat suitability models	v	~
	Current land cover	v	~
	Future land cover		~
	Climate projections		~
	Species/system response to climate change		V
	Novel biotic interactions		~

reflect a diversity of analytical methods and assumptions, but they all attempt to address the obstacles and uncertainties unique to facilitating climate-driven shifts in species' distributions. In this review, we examine the rapidly growing array of connectivity modeling approaches that identify areas most likely to be important routes for species responding to climate change. We then discuss the conceptual and analytical hurdles that remain in this arena. Our review does not summarize discussions on the importance of connectivity for addressing climate change, nor the underlying algorithms and metrics used to model connectivity in general, because both of these topics have been covered elsewhere (eg Gillson *et al.* [2013] and Robillard *et al.* [2015] for the former, and Calabrese and Fagan [2004] and Rayfield *et al.* [2011] for the latter).

Approaches for mapping connectivity under climate change

Research on connectivity to address climate change can be classified into approaches that make use of (1) the projected future ranges of species, (2) climate trajectories and analogs (ie locations that, in the future, will match the climatic conditions of today), (3) existing environmental and climatic gradients, and (4) enduring geophysical features (eg geological formations, mountain ranges, and other landforms; Figure 1; WebTable 1). In examining each of these approaches, we asked: where and how are important areas for biodiversity in the future defined, how are important routes identified, and how are uncertainties associated with model inputs and climate-driven range shifts addressed?

Projected future ranges

One of the most common strategies for modeling connectivity to address climate change is to explicitly model areas of future climatic or habitat suitability for species and then identify potential routes between those areas and currently suitable locations. This approach typically relies on species distribution models (SDMs) that map species' future ranges by identifying where, in the future, currently occupied climatic conditions will be (although mechanistic models could be used as well). The simplest way to link current and potential future ranges is to identify areas of overlap across successive time-steps, thereby maintaining climatic continuity for the focal species over time (eg Vos et al. 2008; Rose and Burton 2009). More complex methods have incorporated dispersal dynamics into SDM-based connectivity via "dispersal chains" that link successively suitable areas within a prescribed dispersal distance (Williams et al. 2005). Others have optimized (eg with network flow) the number of corridors identified by overlapping SDM projections while at the same time minimizing required land area or ensuring species' persistence (Phillips et al. 2008; Alagador et al. 2016). Incorporating SDMs for numerous species can show which areas are important for connectivity across a range of taxa at a continental scale (Lawler et al. 2013).

A major strength of using SDMs for modeling connectivity for climate change is that they explicitly distinguish areas of potential climate suitability based on empirical evidence of where species are now or have been in the past. SDM-based models therefore include explicit destinations, are speciesspecific, and, as such, address the fact that different species are likely to respond uniquely to climate change (Davis and Shaw 2001). Of course, unless many species are modeled, this approach is less suitable for addressing the movement needs of a broad range of species. In addition, SDMs assume that species are well adapted only to the climatic conditions they currently occupy – that is, their realized niches – whereas, in reality, species may have broader climate tolerances, which allow them to adjust as conditions change. The correlations between climate and species' presence that underpin SDMs therefore may not persist in the future, nor may these relationships be adequate for representing range-shift dynamics as they unfold (Pearson and Dawson 2003). SDMs also fail to account for important habitat requirements, including localized suitability for supporting population and metapopulation dynamics (Araújo and Peterson 2012), although mixed SDM-metapopulation models have been proposed (eg Aiello-Lammens et al. 2011; Conlisk et al. 2012). In addition, SDMs do not directly model key mechanisms that can determine species' distributions, such as species' interactions (Araújo and Luoto 2007), although researchers are increasingly coupling SDMs with mechanistic models to address this (eg Fordham et al. 2013; Urban et al. 2016). Finally, projections of future climatic conditions are inherently uncertain (Kujala et al. 2013), and these uncertainties and any errors may be amplified when the projections are incorporated into SDMs that also include uncertainties and inherent assumptions (Fordham et al. 2016).

Climate trajectories and climate analogs

In response to the limitations and uncertainties associated with SDM-based approaches, alternative climate-connectivity modeling strategies – strategies that do not rely explicitly on predicted range shifts – have been developed. Some alternatives instead rely on climate trajectories and climate analogs to produce connectivity maps that identify where and how climatic conditions are expected to shift

across the landscape. As with most SDM-based approaches, those based on climate analogs may explicitly define startand endpoints. For example, Littlefield *et al.* (2017) connected historical climate conditions with analogous future conditions across a human-modified landscape. Alternatively, analogs can be used to map the trajectories of climatic conditions, thereby identifying the pathway a species' range would need to follow to remain within its current temperature conditions over time (Burrows *et al.* 2014).

These coarse-filter models tend not to identify routes for specific species but instead assume that species will most likely follow the same paths as shifting climate conditions. These models are therefore generalizable to a range of species, and allow for community and regional climate reshuffling (Ordonez and Williams 2013). Nonetheless, species will move at different rates and with varying success, depending on a species' dispersal ability, habitat needs, and tolerance of (or ability to adapt to) climate change. As such, climate trajectoryand analog-based connectivity maps may identify potential



Figure 1. Schematics of four types of approaches to model connectivity for climate change. When using projected future ranges, some researchers explicitly identify where species are expected to be in the future and identify routes that link current species' distributions to these locations, whereas others use climate trajectories and analogs to identify where and how climatic conditions will move across the landscape; still others leverage environmental gradients to map routes along which species are expected to move. These may include connections between (a) lower elevations and relatively cooler, higher elevations; (b) downstream areas and headwaters of riparian networks; and/or (c) lower latitudes and higher latitudes. Finally, some researchers identify linkages between similar geophysical features or linkages that connect a high diversity of interspersed land facets, such as: (d) high plateaus, (e) cliffs and steep slopes, (f) north-facing upper slopes, and/or (g) valleys and coves.

linkages that require unrealistic rates of movement or are not spatially aligned with species' niche requirements (Alagador *et al.* 2012; Carroll *et al.* 2015).

Although these approaches do not use SDMs, they are still subject to the uncertainties inherent in climate projections. These uncertainties, though substantial, have been thoroughly explored and are well documented (Kujala *et al.* 2013). Their influence can be minimized by comparing results across multiple climate scenarios, by nesting coarse- and fine-filter models, and by using a suite of climatic metrics for identifying climate analogs (Tingley *et al.* 2014; Carroll *et al.* 2015).

Existing environmental and climatic gradients

Some researchers have sought to bypass the uncertainties associated with using climate projections by instead using existing environmental and climatic gradients to model climate corridors. Such models rely on the "rule of thumb" that species will shift unidirectionally along environmental and climatic gradients as temperatures increase; that is, species are expected to shift from areas that are relatively warmer now to areas that are currently relatively cooler. These connectivity maps span temperature gradients either directly or via close proxies such as elevation, latitude, or physiographic features (eg river networks).

Some climate corridors modeled to capture temperature gradients may explicitly incorporate current climate data, including climate-gradient corridors (Nuñez et al. 2013) that follow unidirectional changes in temperature and riparian climate corridors (Krosby et al. 2014) that prioritize stream networks in which headwaters are cooler than outlets. Other gradient-based approaches do not explicitly incorporate climate data but rely on the fundamental principle that temperatures are generally cooler at higher elevations and latitudes, and that species will shift uphill and toward the poles accordingly. Townsend and Masters (2015), for instance, proposed a latticework corridor system that follows riparian networks both across elevational bands (to facilitate movement) and within elevational bands (to promote population persistence), whereas Anderson et al. (2016) modeled connectivity in the eastern US to prioritize conduits for northward and upward shifts. Most examples of these gradient-based corridors also tend to connect existing habitat patches, such as protected areas or areas in good natural condition. Some of these models explicitly connect habitat patches that differ incrementally in temperature (eg Nuñez et al. 2013; McGuire et al. 2016) so as to provide a network of climatic stepping-stones that would allow species to track shifting climates over time.

In relying only on current climatic conditions to map connectivity, these projection-free approaches seemingly avoid uncertainties of climate projections. Furthermore, there is a conceptual simplicity associated with relying on current climate patterns or easily identified gradients (eg elevation, latitude). The coarse-filter nature of such approaches may also better accommodate the movement needs of a wide range of species and communities, and therefore be more analytically efficient than methods that focus on specific species. Many observed movements under contemporary climate change have indeed followed these "rules of thumb" along coarsegrained climatic gradients toward higher elevations and higher latitudes (Parmesan and Yohe 2003). However, the finer-scaled climatic factors to which species respond (eg water balance) may result in localized shifts that are opposite to these prevailing, broad-scale patterns (Lenoir et al. 2010; Crimmins et al. 2011). Therefore, although models based on existing environmental and climatic gradients circumvent uncertainties in climate-change projections, they do not typically capture finerscaled mechanisms operating on species' persistence, nor can they incorporate rates of climatic changes.

Enduring geophysical features

One final approach to modeling connectivity for climate change relies on mapping and connecting regions with a

diversity of enduring geophysical features, sometimes referred to as "land facets". Underpinning this technique is the theory that various landscape features support unique ecological and evolutionary patterns and processes critical to the maintenance of biodiversity (Anderson and Ferree 2010; Brost and Beier 2012). Moreover, these enduring geophysical features experience change at rates that are orders of magnitude slower than contemporary climate change. Therefore, capturing a diversity of abiotic conditions will likely provide a variety of environments needed to support biodiversity in the future, even as climatic conditions and ecological communities change (Lawler *et al.* 2015).

Brost and Beier (2012) proposed two distinct methods for using land facets to identify range-shift corridors. The first identifies movement corridors with minimal differences in topographic, soil, and geologic conditions along the full length of each corridor, and assumes that some species are particularly well adapted to specific geophysical conditions and therefore their movements will be restricted to these conditions. The second method identifies movement corridors composed of a wide variety of highly interspersed land-facet types, and is based on the theory that many different types of species will be able to disperse through such a corridor because the preferred land facets are in close proximity. Both of these methods are "species-agnostic", in that they do not use information specific to any species. As such, they may identify important linkages for species in general, but they do not expressly distinguish destinations or incorporate the spatiotemporal directionality of range shifts. The reason for this omission is that projected changes in both the direction and location of species' range boundaries are too uncertain to be of use (Brost and Beier 2012).

These projection-free methods seek to bypass the limitations and uncertainties inherent in climate projections and SDMs, but there may be considerable uncertainties associated with the data layers and processes used to define land facets (Lawler and Michalak 2017). Furthermore, although the theory linking biodiversity and land-facet diversity is strong, there is little empirical evidence supporting the assertion that connectivity between and among land facets will facilitate species' movements and other adaptive responses.

The path ahead: conceptual and analytical challenges

Addressing the dynamic nature of climate change over time

Climate change is a dynamic process that progresses continuously, yet the connectivity models meant to address species' responses to this process are rarely, if ever, dynamic. Capturing the variations inherent in climate change remains a major challenge for connectivity modeling and for ecological response modeling in general (Garcia *et al.* 2014; van de Pol *et al.* 2017). Most studies that address species' movements or future ranges either model climate change as a single event at some point in the future or average projected changes over the intervening years, whereas in reality climate change will proceed idiosyncratically, and will be accompanied by extreme events and fluctuations (Garcia *et al.* 2014). These dynamics may compromise the ability of species to successfully track suitable conditions; for example, population persistence during unfavorable climate conditions will be critical for successful range shifts, yet spatial and temporal discontinuities of suitable conditions may be masked when projected changes are averaged over multiple years (Figure 2; Early and Sax 2011).

In response to these challenges, some researchers have modeled climatic conditions with multiple time-steps to approximate the continuous unfolding of changes; these studies have revealed that the relative importance of movement pathways can diminish or expand over time (Littlefield et al. 2017). Other researchers have modeled movement pathways sequentially, by identifying the spatial overlap in projected ranges in sequential slices of time to maintain temporal and spatial continuity of suitable conditions (Rose and Burton 2009; Alagador et al. 2016). From a planning perspective, results from models that include multiple timesteps suggest a role for flexible preserves that can shift across landscapes over time. Nevertheless, these approaches do not truly model climate change as a continuous, dynamic process, nor do they capture other continuous processes such as land-use change and population dynamics, both of which are hurdles for connectivity modeling in general. Ecologists have a long history of focusing on equilibria and ignoring dynamism, but doing so when addressing climate change is particularly problematic.

Identifying future climatic refugia

Locating refugia – the places in current landscapes where species will be able to persist as climate changes - is considered by many to be the "Holy Grail" of modeling connectivity for climate change. Originally a paleoecology concept, the term refugia has traditionally described places where species persisted during past periods of glaciation, as confirmed by the fossil record, genetic analyses, and SDMs (Gavin et al. 2014). That definition has expanded to include areas to which species may retreat and within which they may persist even while the suitability of prevailing climatic conditions declines (Keppel et al. 2012). Refugia operate at multiple spatial and temporal scales: localized, fine-scaled microrefugia are buffered from broader climatic changes and so may remain cooler or wetter than the surrounding areas, whereas macrorefugia describe larger regions that retain increasingly rare climatic conditions (Ashcroft 2010).

Modeling climatic refugia is a rapidly emerging field of research in and of itself. Many methods used to identify refugia are closely related to those used to identify connectivity for climate-driven movement. For example, SDMs, climate ana-



Figure 2. Early and Sax (2011) mapped potential pathways for multiple amphibians, including the California newt (*Taricha torosa*), over four decades of change. Paths were allowed to unfold over adjacent grid cells if climatic suitability in those cells did not drop below species-specific thresholds. In some cases, even transient fluctuations beyond these thresholds caused insufficient time for species to persist while traversing a series of cells, making clear that interdecadal climatic variability may compromise a species' ability to reach projected suitable areas. This suggests that modeling climate-induced movement with greater rather than fewer numbers of time-steps may both minimize the likelihood of overestimating successful movements and more realistically capture population persistence as climate change progresses.

logs, and land-facet diversity have all been used to identify potential refugia and networks of refugia (Figure 3; Vos *et al.* 2008; Maher *et al.* 2017). Furthermore, connectivity models that connect warm patches to cool ones or are based on climatic gradients are likely to capture movement routes to highelevation refugia. To date, however, little work has sought to expressly map future refugia and important movement routes in tandem (but see Vos *et al.* 2008). Leveraging refugia as conservation targets themselves and for their potential role in facilitating movement (eg as stepping-stones) will be important for identifying robust connectivity networks (Morelli *et al.* 2016).

Addressing biological realism

Modeling connectivity in general – even without addressing climate-driven shifts in species' distributions – is an uncertain process (Lawler and Michalak 2017). The uncertainty arises from errors in land-cover data and a lack of knowledge about species' habitats, movements, and tolerance of human activities. Although some types of uncertainty may be quantified and accounted for in analyses and subsequent decision making, other sources of uncertainty are simply inherent limitations in predictive modeling (Urban *et al.* 2016). When attempting to connect landscapes to facilitate climate-driven range shifts, modelers generally lack detailed information about the specific climatic factors that limit species' distributions. Most models rely on annual averages



Figure 3. Maher *et al.* (2017) identified potential refugia in Sierra Nevada montane meadows based on departures from historical climatic conditions, and demonstrated that persistent refugial meadows tended to be higher in elevation and featured more connections to other meadows. Explicitly locating and characterizing the persistence of refugia may therefore highlight important areas of connectivity or, alternatively, may indicate where networks may be tenuous when putative refugia disappear.

and other simple aggregate measures of temperature and precipitation; few capture the extreme events that may facilitate expansions and drive local extinctions. It is these extreme events, as well as changes in moisture, snowpack, and seasonality, that will likely drive range expansions and contractions (Garcia *et al.* 2014).

Moreover, how population dynamics play out at range boundaries - for instance, localized extinctions or the establishment of new populations - may require different approaches to connectivity conservation (Hampe and Petit 2005; Valladares et al. 2014). However, our detection of these events may be biased toward range expansions because contractions are sometimes masked by lingering, localized populations that are destined for extirpation (Dullinger et al. 2012) or simply because there is a greater research effort on leading-edge populations (ie populations along the range edge that is expanding; Hampe and Petit 2005). Improving our understanding of highly variable range boundary dynamics and patterns of both phenotypic plasticity and adaptive capacity across species' ranges (Valladares et al. 2014) may lead to the development of additional connectivity strategies. For example, leading-edge populations that are poised to expand may require linkages to new areas of suitable habitat, whereas improving connectivity between localized populations at the trailing edge may effectively "buy more time" for a species experiencing range contraction.

The distribution of predators, prey, competitors, and facilitators will also affect the timing, direction, and success of species' range shifts, as well as the effectiveness of connectivity-enhancing strategies (Hille Ris Lambers *et al.* 2013). Lags in the shift of biotic habitat elements (eg vegetation communities) may compromise successful range changes. On the other hand, disturbances may reset systems and generate newly available habitat that facilitates successful shifts for some species while simultaneously compromising the persistence of others (Landhäusser et al. 2010). Although large vertebrate species may be capable of moving long distances and traversing landscapes despite unsuitable climatic conditions, plants and smaller animals (including invertebrates) may be considerably more constrained in terms of both how far they can disperse and what terrains they can traverse (Urban et al. 2016).

Although the amount of biological realism in connectivity models could clearly be increased to account for these species-specific and interspecific complexities, a model arguably needs only enough realism to adequately resolve the question being asked of it. Therefore, an additional goal in modeling connectivity to address climate change is determining how much more biological real-

ism is truly needed and where such realism would be most effective in identifying important movement routes for climate-driven range shifts.

Conclusions

Planning for connectivity to facilitate climate-driven range shifts is a relatively new and rapidly evolving area of research. Although a handful of promising approaches have been developed, researchers and planners still face numerous challenges. Even if these challenges are met, however, there is one step in the modeling and planning process that remains largely incomplete. At present, few large-scale connectivity models – and to our knowledge, no connectivity models explicitly designed to account for climate change – have been directly evaluated for long-term effectiveness (Gilbert-Norton *et al.* 2010; Gregory and Beier 2014).

Empirical tests of connectivity plans designed to support climate-driven movements are difficult, if not impossible, to conduct on a relevant timescale. However, spatially explicit population and dispersal simulations are powerful tools for comparing the potential of different landscape configurations and connectivity schemes to support range shifts. For example, Hodgson *et al.* (2012) tested the relative effectiveness of various spatial arrangements of habitat in promoting rapid range shifts across a simulated landscape, and found that landscape patterns resembling corridors or chains of stepping-stones promoted both swift advances and relatively high patch occupancy, more so than increasing habitat patch aggregation alone (ie increasing the proximity of habitat patches within a given area).

CE Littlefield et al.

Importantly, these simulations and other empirical evidence (eg Thomas *et al.* 2012; Bennie *et al.* 2013) serve as reminders that habitat enhancement strategies (eg increasing quality, quantity, or microhabitat representation) that do not expressly add landscape linkages will complement connectivity efforts by reducing extinction risk and supporting metapopulation dynamics and colonization events. Others have simulated land-use change and compared multiple energy-development scenarios to evaluate the robustness of species' habitat networks under a range of climate-change scenarios (eg Dilts *et al.* 2016; Albert *et al.* 2017). Even without simulations, overlaying connectivity maps from multiple models and scenarios to identify commonalities could suggest locations where one may be reasonably confident in the relative importance of such locations for climate-driven movements.

Several researchers have used population genetics to infer landscape permeability and the efficacy of specific corridors for focal species (Marrotte *et al.* 2017), whereas others have directly tracked individuals to validate distribution models, follow movement patterns, and confirm (or refute) corridor use (Gregory and Beier 2014). These techniques hold promise for evaluating connectivity plans designed to promote range shifts but only after, not prior to, on-theground implementation.

Testing connectivity models and strategies is a crucial step toward achieving effective connectivity for species as the globe warms. Nevertheless, as with most conservation problems, researchers and practitioners do not have the luxury of unlimited time to devise the "perfect" approach. Species are already on the move, and some will likely be unable to move far enough or fast enough to track suitable conditions, especially across increasingly fragmented landscapes (Schloss *et al.* 2012; McGuire *et al.* 2016). In the absence of immediate reductions in global atmospheric carbon emissions, facilitating species' movements through applications of the best connectivity tools currently available represents one of the most effective means of preventing climate-driven extinctions.

Acknowledgements

We thank the Wilburforce Foundation (grant number UWAS1811) for supporting this work.

References

- Aiello-Lammens ME, Chu-Agor ML, Convertino M, et al. 2011. The impact of sea-level rise on snowy plovers in Florida: integrating geomorphological, habitat, and metapopulation models. *Glob Change Biol* 17: 3644–54.
- Alagador D, Cerdeira JO, and Araújo MB. 2016. Climate change, species range shifts and dispersal corridors: an evaluation of spatial conservation models. *Methods Ecol Evol* 7: 853–66.
- Alagador D, Triviño M, Cerdeira JO, *et al.* 2012. Linking like with like: optimising connectivity between environmentally-similar habitats. *Landscape Ecol* **27**: 291–301.

- Albert CH, Rayfield B, Dumitru M, and Gonzalez A. 2017. Applying network theory to prioritize multispecies habitat networks that are robust to climate and land-use change. *Conserv Biol* **31**: 1383–96.
- Anderson MG and Ferree CE. 2010. Conserving the stage: climate change and the geophysical underpinnings of species diversity. *PLoS ONE* **5**: e11554.
- Anderson MG, Barnett A, Clark M, *et al.* 2016. Resilient and connected landscapes for terrestrial conservation. Boston, MA: The Nature Conservancy.
- Araújo MB and Luoto M. 2007. The importance of biotic interactions for modelling species distributions under climate change. *Global Ecol Biogeogr* **16**: 743–53.
- Araújo MB and Peterson AT. 2012. Uses and misuses of bioclimatic envelope modeling. *Ecology* **93**: 1527–39.
- Ashcroft MB. 2010. Identifying refugia from climate change. J Biogeogr 37: 1407–13.
- Bennie J, Hodgson JA, Lawson CR, *et al.* 2013. Range expansion through fragmented landscapes under a variable climate. *Ecol Lett* **16**: 921–29.
- Brost BM and Beier P. 2012. Use of land facets to design linkages for climate change. *Ecol Appl* **22**: 87–103.
- Burrows MT, Schoeman DS, Richardson AJ, *et al.* 2014. Geographical limits to species-range shifts are suggested by climate velocity. *Nature* **507**: 492–95.
- Calabrese JM and Fagan WF. 2004. A comparison-shopper's guide to connectivity metrics. *Front Ecol Environ* **2**: 529–36.
- Carroll C, Lawler JJ, Roberts DR, and Hamann A. 2015. Biotic and climatic velocity identify contrasting areas of vulnerability to climate change. *PLoS ONE* **10**: e0140486.
- Conlisk E, Lawson D, Syphard AD, *et al.* 2012. The roles of dispersal, fecundity, and predation in the population persistence of an oak (*Quercus engelmannii*) under global change. *PLoS ONE* 7: e36391.
- Crimmins SM, Dobrowski SZ, Greenberg JA, *et al.* 2011. Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. *Science* **331**: 324–27.
- Davis MB and Shaw RG. 2001. Range shifts and adaptive responses to Quaternary climate change. *Science* **292**: 673–79.
- Dilts TE, Weisberg PJ, Leitner P, *et al.* 2016. Multiscale connectivity and graph theory highlight critical areas for conservation under climate change. *Ecol Appl* **26**: 1223–37.
- Dullinger S, Gattringer A, Thuiller W, *et al.* 2012. Extinction debt of high-mountain plants under twenty-first-century climate change. *Nat Clim Change* **2**: 619–22.
- Early R and Sax DF. 2011. Analysis of climate paths reveals potential limitations on species range shifts. *Ecol Lett* **14**: 1125–33.
- Fordham DA, Akçakaya HR, Brook BW, *et al.* 2013. Adapted conservation measures are required to save the Iberian lynx in a changing climate. *Nat Clim Change* **3**: 899–903.
- Fordham DA, Haythorne S, and Brook BW. 2016. Sensitivity Analysis of Range Dynamics Models (SARDM): quantifying the influence of parameter uncertainty on forecasts of extinction risk from global change. *Environ Modell Softw* **83**: 193–97.
- Garcia RA, Cabeza M, Rahbek C, and Araújo MB. 2014. Multiple dimensions of climate change and their implications for biodiversity. *Science* **344**: 1247579.

- Gavin DG, Fitzpatrick MC, Gugger PF, *et al.* 2014. Climate refugia: joint inference from fossil records, species distribution models and phylogeography. *New Phytol* **204**: 37–54.
- Gilbert-Norton L, Wilson R, Stevens JR, and Beard KH. 2010. A meta-analytic review of corridor effectiveness. *Conserv Biol* 24: 660–68.
- Gillson L, Dawson TP, Jack S, and McGeoch MA. 2013. Accommodating climate change contingencies in conservation strategy. *Trends Ecol Evol* 28: 135–42.
- Gregory AJ and Beier P. 2014. Response variables for evaluation of the effectiveness of conservation corridors. *Conserv Biol* **28**: 689–95.
- Hampe A and Petit RJ. 2005. Conserving biodiversity under climate change: the rear edge matters. *Ecol Lett* **8**: 461–67.
- Heller N and Zavaleta ES. 2009. Biodiversity management in the face of climate change: a review of 22 years of recommendations. *Biol Conserv* 142: 14–32.
- Hille Ris Lambers J, Harsch MA, Ettinger AK, *et al.* 2013. How will biotic interactions influence climate change–induced range shifts? *Ann NY Acad Sci* **1297**: 112–25.
- Hodgson JA, Thomas CD, Dytham C, *et al.* 2012. The speed of range shifts in fragmented landscapes. *PLoS ONE* 7: e47141.
- Keppel G, Van Niel KP, Wardell-Johnson GW, *et al.* 2012. Refugia: identifying and understanding safe havens for biodiversity under climate change. *Global Ecol Biogeogr* **21**: 393–404.
- Krosby M, Tewksbury J, Haddad NM, and Hoekstra J. 2010. Ecological connectivity for a changing climate. *Conserv Biol* 24: 1686–89.
- Krosby MB, Norheim RA, Theobald DM, and McRae BH. 2014. Riparian climate-corridors: identifying priority areas for conservation in a changing climate. Seattle, WA: Climate Impacts Group, University of Washington.
- Kujala H, Moilanen A, Araújo MB, and Cabeza M. 2013. Conservation planning with uncertain climate change projections. *PLoS ONE* **8**: e53315.
- Landhäusser SM, Deshaies D, and Lieffers VJ. 2010. Disturbance facilitates rapid range expansion of aspen into higher elevations of the Rocky Mountains under a warming climate. *J Biogeogr* **37**: 68–76.
- Lawler JJ and Michalak JL. 2017. Planning for climate change without climate projections? In: Karieva P, Sillman B, and Marvier M (Eds). Effective conservation science: data not dogma. Oxford, UK: Oxford University Press.
- Lawler JJ, Ackerly DD, Albano CM, *et al.* 2015. The theory behind, and the challenges of, conserving nature's stage in a time of rapid change. *Conserv Biol* **29**: 618–29.
- Lawler JJ, Ruesch AS, Olden JD, and McRae BH. 2013. Projected climate-driven faunal movement routes. *Ecol Lett* **16**: 1014–22.
- Lenoir J, Gégout J, Guisan A, *et al.* 2010. Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. *Ecography* **33**: 295–303.
- Littlefield CE, McRae BH, Michalak JL, *et al.* 2017. Connecting today's climates to future climate analogs to facilitate movement of species under climate change. *Conserv Biol* **31**: 1397–408.
- Maher SP, Morelli TL, Hershey M, *et al.* 2017. Erosion of refugia in the Sierra Nevada meadows network with climate change. *Ecosphere* **8**: e01673.

- Marrotte RR, Bowman J, Brown MG, *et al.* 2017. Multi-species genetic connectivity in a terrestrial habitat network. *Movement Ecol* **5**: 21.
- Mazaris AD, Papanikolaou AD, Barbet-Massin M, *et al.* 2013. Evaluating the connectivity of a protected areas' network under the prism of global change: the efficiency of the European Natura 2000 Network for four birds of prey. *PLoS ONE* **8**: e59640.
- McGuire JL, Lawler JJ, McRae BH, *et al.* 2016. Achieving climate connectivity in a fragmented landscape. *P Natl Acad Sci USA* **113**: 7195–200.
- Morelli TL, Daly C, Dobrowski SZ, *et al.* 2016. Managing climate change refugia for climate adaptation. *PLoS ONE* **11**: e0159909.
- NPS (US National Park Service). 2010. National Park Service climate change response strategy. Fort Collins, CO: NPS.
- Nuñez TA, Lawler JJ, McRae BH, *et al.* 2013. Connectivity planning to address climate change. *Conserv Biol* **27**: 407–16.
- Ordonez A and Williams JW. 2013. Projected climate reshuffling based on multivariate climate-availability, climate-analog, and climate-velocity analyses: implications for community disaggregation. *Climatic Change* **119**: 659–75.
- Parmesan C and Yohe G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37–42.
- Pearson RG and Dawson TP. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecol Biogeogr* **12**: 361–71.
- Phillips SJ, Williams P, Midgley G, and Archer A. 2008. Optimizing dispersal corridors for the Cape Proteaceae using network flow. *Ecol Appl* **18**: 1200–11.
- Rayfield B, Fortin MJ, and Fall A. 2011. Connectivity for conservation: a framework to classify network measures. *Ecology* **92**: 847– 58.
- Robillard CM, Coristine LE, Soares RN, and Kerr JT. 2015. Facilitating climate-change-induced range shifts across continental land-use barriers. *Conserv Biol* **29**: 1586–95.
- Rose NA and Burton PJ. 2009. Using bioclimatic envelopes to identify temporal corridors in support of conservation planning in a changing climate. *Forest Ecol Manag* **258**: S64–74.
- Schloss CA, Nuñez TA, and Lawler JJ. 2012. Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. *P Natl Acad Sci USA* **109**: 8606–11.
- Thomas CD, Gillingham PK, Bradbury RB, *et al.* 2012. Protected areas facilitate species' range expansions. *P Natl Acad Sci USA* **109**: 14063–68.
- Tingley MW, Darling ES, and Wilcove DS. 2014. Fine- and coarsefilter conservation strategies in a time of climate change. *Ann NY Acad Sci* **1322**: 92–109.
- Townsend PA and Masters KL. 2015. Lattice-work corridors for climate change: a conceptual framework for biodiversity conservation and social-ecological resilience in a tropical elevational gradient. *Ecol Soc* **20**: art1.
- Urban MC, Bocedi G, Hendry AP, *et al.* 2016. Improving the forecast for biodiversity under climate change. *Science* **353**: aad8466.
- Valladares F, Matesanz S, Guilhaumon F, *et al.* 2014. The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. *Ecol Lett* **17**: 1351–64.

- van de Pol M, Jenouvrier S, Cornelissen JHC, and Visser ME. 2017. Behavioural, ecological and evolutionary responses to extreme climatic events: challenges and directions. *Philos T Roy Soc B* **372**: 20160134.
- Vos CC, Berry P, Opdam P, *et al.* 2008. Adapting landscapes to climate change: examples of climate-proof ecosystem networks and priority adaptation zones. *J Appl Ecol* **45**: 1722–31.
- WGA (Western Governors' Association). 2008. Wildlife corridors initiative report. Denver, CO: WGA.



Highwayman fly hijacks fierce trap-jaw ants

The genus of blow flies *Bengalia* includes more than 70 species, which are found in the world's African and Asian tropics. *Bengalia* flies are best known for their remarkable highwayman-like habit of stealing ant eggs, larvae, and pupae, as well as various prey being transported by the ant workers. The flies also attack termite workers emerging from damaged nests.

Another group of combative insects, the trap-jaw ants (genus *Odontomachus*), have specialized spring-loaded mandibles that snap shut at some of the fastest speeds in the animal kingdom (64 m s–1) and generate forces over 300 times their body weight. More than 70 *Odontomachus* species, found in the Asian and American tropics, are known for their powerful mandibles, used for predation and defense.

What happens when two such fierce insects (whose geographic ranges show considerable overlap) encounter each other? We observed foraging *B varicolor* flies pouncing on disturbed *O monticola* colonies to steal and consume ant pupae. The predatory fly can easily subdue the ant, which is occupied with carrying its offspring in its power-amplified mouthparts; what's more, the ant's poisonous sting is unable to reach the fly.

Yet the causes and consequences of this fly–ant interaction remain unclear. Can the flies detect alarm and/or trail pheromones from the ants? What are the fitness costs to the ants of being hijacked? The answers likely depend on local abundances of both insects.



Williams P, Hannah L, Andelman S, et al. 2005. Planning for climate change: identifying minimum-dispersal corridors for the Cape Proteaceae. Conserv Biol 19: 1063–74.

Supporting Information

Additional supporting information, web-only material may be found in the online version of this article at http://onlinelibrary. wiley.com/doi/10.1002/fee.2043/suppinfo



Gao Chen¹ and Guillaume Chomicki² ¹Kunming Institute of Botany, Chinese Academy of Sciences, Kunming, China; ²Department of Plant Sciences, University of Oxford, Oxford, UK doi:10.1002/fee.2054