Climate Velocity Can Inform Conservation in a Warming World

Brito-Morales, Isaac; Molinos, Jorge Garcia; Schoeman, David S.; Burrows, Michael T.; Poloczanska, Elvira S.; Brown, Christopher J.; Ferrier, Simon; Harwood, Tom D.; Klein, Carissa J.; McDonald-Madden, Eve; Moore, Pippa J.; Pandolfi, John M.; Watson, James E. M.; Wenger, Amelia S.; Richardson, Anthony J.

Published in:
Trends in Ecology & Evolution

Publication date:
2018

Trends in Ecology and Evolution

Climate velocity can inform conservation in a warming world

--Manuscript Draft--

Manuscript Number:	TREE-D-17-00340R1
Article Type:	Review
Keywords:	climate velocity; climate-analogue velocity; climate change; conservation; biodiversity

Corresponding Author:	Isaac Brito-Morales Brisbane, AUSTRALIA
First Author:	Isaac Brito-Morales
Order of Authors:	Isaac Brito-Morales
	Jorge García Molinos
	David S Schoeman
	Michael T Burrows
	Elvira S Poloczanska
	Christopher J Brown
	Simon Ferrier
	Tom D Harwood
	Carissa J Klein
	Eve McDonald-Madden
	Pippa J Moore
	John M Pandolfi
	James E Watson
	Amelia S Wenger
	Anthony J Richardson

Abstract:	Climate change is shifting species' ranges. Simple predictive metrics of range shifts, such as climate velocity, that do not require extensive knowledge and data on individual species could help guide conservation. We review research on climate velocity, describing the theory underpinning the concept and its assumptions. We highlight how climate velocity has already been applied in conservation-related research, including climate residence time, climate refugia, endemism, historic and projected range shifts, exposure to climate change, and climate connectivity. Finally, we discuss ways to enhance the use of climate velocity in conservation, through tailoring it to be more biologically meaningful, informing design of protected areas, conserving ocean biodiversity in three dimensions, and informing conservation actions.

Trends:

- Climate velocity is a simple metric that describes the speed and direction of climate movement at any point in space.
- Climate velocity is providing information about climate change relevant for conservation, including the study of protected areas, novel and/or disappearing climates, rates of endemism, and range shifts.
- To better inform conservation, climate velocity can be tailored to be more biologically meaningful through the addition of species' dispersal capabilities, physiological tolerance, and potential routes of movements
- There is untapped potential for using climate velocity and climate-velocity trajectories in informing design of protected areas and their networks, conserving ocean biodiversity in three dimensions, and in informing conservation actions.
- To stimulate future research using climate velocity, we introduce the R package *vocc*.

Climate velocity can inform conservation in a warming world

Authors

Isaac Brito-Morales[1,2], Jorge García Molinos[3], Dave S. Schoeman[4,5], Michael T. Burrows[6], Elvira S. Poloczanska[7,8], Christopher J. Brown[9], Simon Ferrier[10], Tom D. Harwood[10], Carissa J. Klein[1], Eve McDonald-Madden[1,11], Pippa J. Moore[12,13], John M. Pandolfi[14], James E. Watson[1,15], Amelia S. Wenger[1] and Anthony J. Richardson[2,16]

[1]School of Earth and Environmental Sciences, The University of Queensland, St Lucia, Queensland, Australia
[2]CSIRO Oceans and Atmosphere, EcoSciences Precinct, Dutton Park, Queensland, Australia
[3]Arctic Research Center, Hokkaido University, Hokkaido, Japan
[4]School of Science and Engineering, University of the Sunshine Coast, Maroochydore, Queensland, Australia.
[5]Centre for African Conservation Ecology, Department of Zoology, Nelson Mandela University, Port Elizabeth, South Africa
[6]Scottish Association for Marine Science, Oban, UK
[7]The Global Change Institute, The University of Queensland, St Lucia, Queensland, Australia
[8]Alfred Wegener Institute for Polar and Marine Research, Integrative Ecophysiology, Bremerhaven, Germany
[9]Australian Rivers Institute, Griffith University, Nathan, Queensland, Australia
[10]CSIRO Land and Water, Canberra, ACT, Australia
[11]ARC Centre of Excellence for Environmental Decisions, School of Biological Sciences, The University of Queensland, St Lucia, Australia
[12]Institute of Biological, Environmental and Rural Sciences, Aberystwyth University, Aberystwyth SY23 3FG, UK

[13]Centre for Marine Ecosystems Research, Edith Cowan University, Joondalup, WA 6019, Australia

[14]School of Biological Sciences, Australian Research Council Centre of Excellence for Coral Reef Studies, The University of Queensland, St Lucia, Queensland, Australia

[15]Wildlife Conservation Society, Global Conservation Program, Bronx, NY, USA

[16]Centre for Applications in Natural Resource Mathematics, School of Mathematics and Physics, University of Queensland, St Lucia, Queensland, Australia

Corresponding author: Brito-Morales, I. (i.britomorales@uq.edu.au)

Keywords: climate velocity; climate-analogue velocity; climate change; conservation; biodiversity

Abstract

Climate change is shifting species' ranges. Simple predictive metrics of range shifts, such as climate velocity, that do not require extensive knowledge and data on individual species could help guide conservation. We review research on climate velocity, describing the theory underpinning the concept and its assumptions. We highlight how climate velocity has already been applied in conservation-related research, including climate residence time, climate refugia, endemism, historic and projected range shifts, exposure to climate change, and climate connectivity. Finally, we discuss ways to enhance the use of climate velocity in conservation, through tailoring it to be more biologically meaningful, informing design of protected areas, conserving ocean biodiversity in three dimensions, and informing conservation actions.

Simple climate metrics could help conservation in a changing climate

Climate change is likely to become the most serious threat to biodiversity this century [1, 2]. In fact, anthropogenic climate change, initiated in the Industrial Revolution, has already affected ecological systems from individual organisms to biomes [3, 4], and has influenced >80% of all biological processes [5]. Although ecological responses to climate change are numerous, complex and multi-faceted, probably the most fundamental is the spatial redistribution of global biodiversity [3]. Such species range shifts, in response to a changing climate, have been observed across terrestrial and marine ecosystems during the current warming period [6-8] and since the last glacial maximum [9, 10]. Understanding the processes underpinning range shifts and predicting their potential outcomes is needed to inform conservation, and reduce risks to food security, human health, and the viability of numerous industries that depend on ecosystem services, including forestry, fisheries, and eco-tourism.

Mechanisms underpinning range shifts are a blend of a species' exposure, sensitivity and vulnerability to climate change, combined with its adaptive capacity [11]. Of these characteristics, only exposure to climate change might be considered relatively generic across species, with other traits being specific to individual species or populations. But detailed physiological, ecological and evolutionary data are missing for most species, especially in the tropics and much of the global ocean [12], and current research priorities make collection of such data increasingly difficult [13, 14]. This leaves conservation and management agencies to make decisions with whatever alternative tools are available. Threats to biodiversity posed by climate change have thus traditionally been quantified using rates of warming or cooling, temperature anomalies, or degree heating weeks [15]. What these simple indices do not convey is the relative likelihood that a species might escape the threat of climate change by shifting its distribution. A promising solution that retains generality, but conveys more ecologically relevant information is the velocity of climate change, or more simply, climate velocity [16-18]. Climate velocity is a metric that uses freely-accessible environmental and climate data, without the need for detailed ecological knowledge [19], to approximate the observed shifts in species' distributions [20-23]. Climate velocity thereby provides a simple and intuitive measure of threats to biodiversity posed by climate change [24] and as such, in is simplest form, is not bespoke for particular species.

Here, we explore the meaning, utility and application of climate velocity, with a particular focus on the potential for its use to guide conservation under a changing climate. We begin by defining the concept of climate velocity, as there are several formulations with different conceptual underpinnings. This leads to a summary of the methodological aspects and caveats that need to be considered when using climate velocity. We then describe the different applications of climate velocity that have provided new insights into many areas of climate-change ecology. Next, we look to the future and explore four ways to improve the utility of climate velocity in conservation. We focus on simple metrics that use raw climate variables, and do not consider velocities that can be calculated from species distribution models or assemblage models that scale climate space by biological data (e.g., Generalized Dissimilarity Modelling) [25]. This review is targeted at ecologists seeking to understand how climate change could affect communities, and for conservation practitioners wanting to include climate change in their planning.

What is climate velocity?

Climate velocity is a vector that describes the speed and direction that a point on a gridded map would need to move to remain static in climate space (e.g., to maintain an isoline of a given variable in a univariate environment) under climate change (see Glossary). From an ecological perspective, climate velocity can be conceptualized as the speed and direction in which a species would need to move to maintain its current climate conditions under climate change (see Box 1). For this reason, climate velocity can be considered the potential exposure to climate change faced by a species, if the climate moves beyond the physiological tolerance of a local population. Despite the intuitive ecological relevance, however, climate velocity is based solely on environmental variables and not on species data (Box 1).

Two major approaches to calculating climate velocity have emerged: viz., “local” climate and “climate-analogue” velocities (Figure 1). Local climate velocity is the original metric proposed in 2009 by Loarie *et al.* [16]. To calculate local climate velocity at a location – how far and in which direction the isoline of an environmental variable would move – only the rate of change of a variable (e.g., temperature) through time (i.e., the trend, usually estimated as the regression slope), and the corresponding spatial gradient of that variable, are needed. The spatial gradient represents the complexity of the climate landscape, its magnitude calculated as the length of a vector resulting from the weighted sum of the latitudinal and longitudinal pairwise differences in values of the climate variable between a focal cell and its nearest neighbours (Figure 1A). The associated angle of the vector gives the direction of the spatial gradient. Directions of climate velocity are reversed relative to those of the spatial gradient to reflect response expectations (e.g., in a warming climate, movement towards cooler locations). It is this dependence on neighbouring (local) cells for the estimation of the spatial gradient in climate that gives local climate velocity its name.

Climate-analogue velocity [26] emerged as an extension of the climate analogue concept [27] – i.e., the identification of points in space with climates sufficiently similar to those of the points under consideration (Figure 1). Euclidean distances are often used as measures of multivariate climatic dissimilarity, climate analogy being set by reference to a dissimilarity threshold defined either subjectively [28, 29] or using regional statistics (e.g., 95th percentile of the minimum Euclidean distance between each future climate and all current climates) [26, 30]. Importantly, the selected threshold is constant and common to all local climates. When the points under consideration represent the current climate, and their analogues are sought in a future climate, the geographic distance between points can be divided by the time separating the periods to compute a speed of climate change. The direction for the climate-analogue velocity is provided by the relative positions of the original point and its future analogue (Figure 1B). Climate-analogue velocity can be further conceptualized in two related but distinct ways: “*forward” analogue velocity*, the original formulation, and *“backward” analogue velocity*, which is the inverse of forward velocity ([28], Glossary).

Local and climate-analogue velocities have been used in different situations. Local climate velocity has usually been used for exploring potential responses of biota to single variables, usually temperature [31], but sometimes precipitation [32]. This metric has been favoured by ecologists when gradients are smooth and where there is one main variable driving change (e.g., in the open ocean, Figure S1). Local climate velocity can be constrained by species requirements for particular habitat features, such as being limited to coastal marine regions by the need for light on the sea bottom, or substratum types for reef formation, or intertidal zones [33]. By contrast, climate-analogue velocity has usually been used with multiple variables [34]. It has greater ecological realism in complex environments with contrasting climatic gradients, and is favoured by ecologists dealing with species with multiple needs. For example, on land, temperature and rainfall have often been analysed in multivariate space using climate-analogue velocity (Figure S1). Irrespective of the climate-velocity metric used and data availability, researchers should be aware of several associated caveats (Box 2), and a suite of methodological aspects, including which environmental variables to use, their time and space scales, and how to combine multiple variables (Box 3).

To encourage the robust use of climate velocity in the ecological and conservation research communities, we provide two resources. The first is a collection of R functions aggregated into a package, *vocc*, that is freely available on GitHub (https://github.com/cbrown5/vocc). This package calculates the local climate velocity for univariate environmental datasets, on local to global scales (see the SOM of Hamann *et al.* [28] for R code for climate-analogue velocity). The second resource is a list of all freely available environmental datasets (and their websites) that have been used in climate-velocity research (Table S1 supplemental online information).

Current applications of climate velocity

Figure S2 shows conceptual relationships among different applications of climate velocity, highlighting key references, and common applications between local climate and climate-analogue velocity. There are six main areas where local and climate-analogue velocities have provided new insights into climate-change ecology.

1. Climate residence time

From its inception, local climate velocity was used to estimate the residence time of current climates in protected areas and different biomes under climate change [16, 17]. Large protected areas, especially in hilly areas, are likely to continue to provide climate space for resident species into the next century (because air temperature decreases with altitude), but small reserves and reserves in flatter areas are likely to fail to do so (see also Box 1 and Box 3). The latter conclusion should, however, be viewed with caution: values of climate residence time can be alarmingly small, but might not reflect individual species' residence times, because the local climate might not approach critical thermal limits for a species, a species' thermal range might be large, or a species might be able to adapt behaviourally (or otherwise) thereby persisting in a climate that might otherwise be inhospitable [33, 35]. Nevertheless, the primary conservation-related recommendations from studies of climate residence time seem defensible. They include emissions reductions to slow the rate of climate change, and expanding networks of protected areas and including more mountainous terrain [36] to increase the residence time of climates (and therefore migrating species).

2. Climate refugia and rates of endemism

Areas of low local climate and climate-analogue velocities can be considered candidate areas for protection [24, 37] because they are likely to contain a consistent suite of species and their ecological interactions as they evolved together in a slowly moving climate. Such areas are often called climate refugia, and have been linked with high levels of endemism [38]. For example, Sandel *et al.* [9] related local climate velocity between the last glacial maximum and current climates, and used these to explore endemism of amphibians, mammals and birds. Relationships between climate velocity and rates of endemism were weakest for wide-ranging species and strongest for narrow-ranged species, suggesting that areas of slow climate velocity provide important refugia for biodiversity under climate change. Subsequent studies on endemic species of insects and mammals [39], birds [40, 41], and plants [42, 43] confirm these patterns at a regional scale, and patterns seem to hold even at local scales within freshwater streams [44].

3. Historic range shifts

The magnitude and direction of local climate velocity explains range shifts in many species on land [22] and in the ocean [7, 21, 22, 45-47]. For example, on land, global meta-analysis of over the past 40 years showed that terrestrial species tracked local climate velocity in response to warming to higher latitudes and higher elevation [48]. In marine systems, extensive data on marine species (128 million individual fish and invertebrate records across 360 harvested species) around North America closely track local climate velocity, both horizontally and vertically in the ocean, over the past 50 years [20]. We expect greater agreement between climate velocity and species distribution shifts in homogenous systems such as the open ocean and continental plains. Such homogenous systems pose fewer constraints on movement because species are more able to follow local climate velocity, whereas heterogeneous and complex systems have barriers to dispersal and movement that can constrain distribution shifts. In such environments, estimates of climate velocity can be modified – see Section *Tailoring climate velocity to be more biologically meaningful*. Note also that even in relatively homogenous regions, divergence among climate variables mediating species' distributions might complicate responses.

4. Exposure of organisms to climate change, migration velocities and the formation of novel communities

Because climate velocity quantifies the speed and direction of a changing climate, it also quantifies the exposure of a species to climate change [19, 29]. Recently, Ordonez *et al.* [30] used local climate velocity as one of three mechanisms driving the reshuffling of species and emergence of novel communities under climate change, the other two being climate novelty (opening of new suitable environments) and divergence (discrepancy in the direction of change among gradients of different climate variables in relation to a species' niche). As elsewhere [24, 26, 49], slow local and climate-analogue velocities were associated with regions of strong spatial gradients in environmental conditions (e.g., mountains) and assumed to be least-exposed to climate change (i.e., requiring shorter dispersal distances to track changes in climate). Climate exposure can also be modified by climate connectivity (see below) [24, 29, 50]. In this case, exposure relates to the cost of moving through climatically heterogeneous land- or seascapes, possibly accounting for other non-climate drivers conditioning dispersal [29].

5. Climate-velocity trajectories and climate connectivity

To address Loarie *et al.'s* [16] caution that local climate velocity is discontinuous, Burrows *et al.* [24] developed climate-velocity trajectories by moving climate "tracers" between neighbouring grid cells based on the local climate velocity. Climate-velocity trajectories thus track specific climate conditions through time as continuous paths (see Box 4 Figure I). Spatially aggregated patterns of climate-velocity trajectories suggest changes in species richness with climate, and notably highlight areas that might receive few or no climate migrants through lack of connections to warmer places (climate 'sources': locally warm areas such as equatorward-facing coastlines on land or poleward-facing coastlines in the ocean), and areas where there might be local extirpations through lack of connections to cooler areas (climate ‘sinks’: locally cool areas such as mountain tops on land and equatorward facing coastlines in the ocean) (e.g. [2, 22]).

6. Projected range shifts with climate change

As climate velocity is an indicator of the speed at which species’ range shifts track climate change – potentially the maximum possible rate of range shift when dispersal is not a limiting factor – climate-driven changes in the geographical distribution of species can be simply predicted by forward (or backward) projection of their climate envelopes (see Glossary) following the speed and direction of local or analogue climate velocities. This approach has been combined with species’ thermal tolerances and depth preferences to predict changes in distribution of marine species. Applying this approach for >13,000 marine species, García Molinos *et al.* [33] found that biodiversity would decrease in equatorial regions, but increase in others, and there would be a spatial homogenization of biodiversity by 2100. Recent observations of marine communities confirm those results in response to climate change [51, 52]. However, the likelihood of a response, and a subsequent shift in range mirroring climate velocity, is species-specific. For example, opportunities for the expansion and risk of contraction of a geographical range will depend on changes in the local climate space relative to a species’ physiological tolerances (see Box 1, Figure II). Even if a geographical shift is triggered by changes in climate, different dispersal capacities of species result in range shifts that keep pace with, lag or even exceed rates of climate displacement [53-60]. Range shifts will also depend on the interaction between climate change and external directional forces. In a recent global meta-analysis [61], statistical models combining the effect of climate velocity and its alignment with ocean currents explained a significantly higher proportion of the variance in observed range shifts for marine species globally than models based only on climate.

Enhancing use of climate velocity in conservation

Although recent applications of climate velocity have provided new insights into climate-change ecology, they have so far made only generic recommendations concerning conservation [62-64]. Here, we explore four research areas where we believe that climate velocity can be integrated more directly into biodiversity conservation under a changing climate.

1. Tailoring climate velocity to be more biologically meaningful

In its simplest form, climate velocity is a purely physical metric, so the utility of climate velocity in conservation could be improved through the addition of information that can better represent underlying ecological processes (Figure 2). First, a more realistic spatial extent can be defined for climate-analogue velocity algorithms by limiting the pool of potential analogues to those locations within the distance that species can be expected to cover over a given period based on their dispersal capability (Figure 2B). If this information on dispersal capacity is not available, alternative proxies might be suitable. For example, the limits of reported range expansion and contraction rates can be used to limit the analogue search radius [50]. Similar considerations apply to the spatial resolution of the climatic layers defining the spatial units for local climate velocities (e.g., resolutions that are too fine could result in local climate sinks that are easily avoided in reality by a widely-dispersing species). Second, analogous environmental conditions can be made more relevant to a species by considering the climate tolerance of a species, or the historical variability in local climate conditions [50] (Figure 2C). Last, climate velocity (local and analogue approaches) and climate-velocity trajectories miss information about the potential for a species to depart from the minimum-distance path in search of routes less exposed to changes in climate [29, 50] or other non-climate factors conditioning dispersal, such as habitat permeability [65], or directional forces, such as wind and ocean currents [61]. Least-cost paths [29, 65] and randomized shortest paths [50] linking present and future analogues can be used for this purpose, the latter having the advantage of allowing a degree of network exploration rather than a single, unidirectional source-to-destination pathway [66]. This reflects a more realistic scenario, where the location of the future climate analogue and the optimal route to reach it are unknown *a priori*.

Changes in climate can also manifest differently depending on season, and this seasonal signal can be obscured in annual means that are usually used in calculating climate velocity. Tailoring climate velocity to match temporal windows of biological processes or life stages could therefore provide more meaningful information for conservation (see example in Figure S3). For example, maximum and/or minimum monthly temperature or precipitation [26, 32, 34, 67] can be used to calculate local or climate-analogue velocities when seasonal processes are under consideration [68]. Further, analysis of the seasonal local climate velocity could be complemented with the shift in the timing of fixed temperatures to capture the onset or termination of seasonal processes [18]. The utility of combining metrics of climate velocity and timing has not yet been investigated.

Species can "escape" climate change by exploiting specific microclimates. For example, mammals could spend more time underground in burrows, or marine invertebrates could spend more time in the sediment than exposed. Thus, incorporating such microhabitats or local climate refugia into climate velocity might also increase biological realism. But how this might be achieved is an open question, and many challenges remain. For example, microclimate refugia manifest at scales finer than those resolved in climate velocities, yet the local climate heterogeneity generated by such microclimates can be much greater than macroclimatic trends [69]. Microhabitats could also be more important in two-dimensional environments (e.g. terrestrial landscapes) than well-mixed, three-dimensional pelagic environments, at least for large organisms.

It should be noted that in each instance, adding biological realism to climate velocity comes at a cost. The current lack of biological information in climate velocity in its simplest form confers generality across a broad range of species. However, the more climate velocity is tailored to be more biologically meaningful, the more specific the metric becomes to the species under consideration. Thus, the path of increasing biological realism moves climate velocity towards species distribution models or other species-specific modelling approaches that potentially have better predictive ability, but require more species-specific information and are less generally applicable.

2. Informing design of protected areas and their networks

Protected areas need to be considered within a holistic ecosystem-based management approach that recognizes the interactive and cumulative impact of human activities [70]. However, the consideration of climate change in the design and evaluation of protected areas is still in its infancy [71]. Here, climate velocity might be useful in several ways. First, climate velocity identifies regions where climate conditions are changing rapidly, or are projected to do so in the future. These regions might correspond to those where distribution shifts are more likely, particularly at range boundaries or for range-restricted species, potentially moving species out of the protected areas designed to protect them [72, 73]. Further, current climate-velocity patterns can differ strongly from those projected for the future, highlighting the challenge of anticipating effects of a dynamic climate when designing static networks of protected areas (see Box 3). Second, climate velocity can be used to estimate climate residence time (Glossary) of different protected areas across a network (Box 3), indicating the required pace of adaptation to climate change. Areas of long climate residence times correspond to areas of low climate velocity. On land, however, areas of long residence times tend to be in mountainous terrain, perhaps contributing to the problem of residual reserves, that is, areas where conservation impact is low because the land is unsuitable for conversion or extraction of natural resources [74, 75]. Third, climate velocity can also be interpreted in terms of the opportunities for range expansions via dispersal and colonization from local populations at the leading edge of a species' distribution. Here, establishing the connectivity between current and future climates will be important for anticipating whether the existing network of protected areas will capture those expansions. For example, climate-velocity trajectories [24] used for this purpose can reveal emergent classes of isotherm shifts [76], which could be relevant to biology and ultimately used to inform conservation actions (Box 3).

3. Conserving ocean biodiversity in three dimensions

In the ocean, climate velocity has mainly been applied to surface temperatures (e.g., [33, 50, 77]), which are probably relevant for epipelagic (0-200 m) marine groups, including all photosynthetic organisms that need to remain within the sunlit zone (the top 200 m). But in the open ocean, mesopelagic (200-1000 m) and bathypelagic (1000-4000 m) marine groups live below this sunlit zone, and the magnitude and direction of climate velocity might change with depth, with important implications for conservation [78, 79] (Figure S4). For example, although there is less warming in the deep ocean relative to the surface [80], spatial gradients are likely to be gentler at depth, so it is unclear how the climate velocity might change with depth. Moreover, the direction of climate velocity could differ with depth, according to the spatial gradient of temperature in different ocean layers (Figure S4, also see the SOM of Hiddink *et al.* [21]), implying that species distributions might move in different directions with depth. Different horizontal speeds and directions of climate velocity with depth would influence whether organisms at different depths remain within a particular marine protected area with climate change [81], and whether communities at different depths and that interact, remain intact.

Not only can climate velocity be applied in horizontal slices in the ocean, but to the seafloor. Movements of organisms on the seafloor are restricted to a two-dimensional surface, as they are on land, and conventional two-dimensional climate velocity is therefore appropriate. As terrestrial species move to higher (cooler) elevations with warming, marine organisms on the seafloor have been observed to move to deeper (cooler) water with warming [20] (Figure S4). A pertinent conservation issue concerning seafloor communities is how best to conserve seamounts, which have high levels of endemism and vertical habitat zonation [82], as mountains do on land. Applying local-climate velocity to seamounts could provide new insights into how these unique communities could respond to climate change. Seamounts also function as stepping stones for many animals across the abyssal plain [83], as mountains do on land. Applying climate-analogue velocity could provide new insights into how animals might move between seamounts in response to climate change, and help inform networks of protected areas for seamounts.

Movements of organisms at the sea surface, at different ocean depths, or on the seafloor are restricted to two dimensions, and conventional climate velocity is therefore appropriate. However, movement of organisms in the open ocean is different, as organisms can move vertically through the water to maintain their environmental conditions. Climate velocity can thus be calculated purely vertically, from the surface to seafloor. This vertical climate velocity can be used to make projections of vertical shifts of open ocean species under climate change (Figure S4). Similarly, vertical velocity could be calculated for other variables (e.g., shoaling of oxygen or pH [84], but see Boxes 2 and 3).

So far, we have considered horizontal and vertical climate velocity independently. Most organisms in the open ocean, however, are not constrained to moving only horizontally or vertically in response to climate change, but could simultaneously move horizontally and vertically to maintain their current temperature conditions. Thus, a final advance in the open ocean would be to combine the horizontal and vertical velocities into a truly three-dimensional climate velocity.

4. The potential of climate velocity to inform conservation actions

Climate-velocity trajectories provide considerable scope to inform conservation actions (see Table S2 for trajectory classes [24, 76] and a summary of potential implications for species and conservation actions). For example, climate source areas (i.e., regions of novel climate conditions) might face loss of indigenous biodiversity through emigration of species with good dispersal ability, and in some cases extirpation of some species with short dispersal abilities that cannot track their climate niche. In climate source areas, conservation actions might be focused not only on monitoring alien invasive species that might occupy emptying niches, but also ensuring that indigenous species have the ability to emigrate (Table S1). By contrast, in climate sink areas (i.e., where climates converge and sometimes disappear), species must adapt to new climate or face extirpation, and must also cope with climate-immigrant species that bring novel interactions. In climate sinks, conservation actions might be focused on potential mitigation of other anthropogenic stressors to aid adaptation, and in extreme cases, assisted migration could be considered [85] (Table S2). Areas where climate changes little (e.g., slow and non-moving climate-velocity trajectory classes) are key for conservation because they usually provide refuges from climate change and have high rates of endemism [9]. Although these areas are likely to be the main focus to protect biodiversity, they might also be good places to release species translocated from climate sinks (Table S2).

Concluding remarks

The growing literature on climate velocity demonstrates that it can provide valuable information on the magnitude and direction of species' range shifts under a changing climate. This simple index, based on environmental data with no physiological information, is providing new ecological insights. We hope that this review stimulates wider consideration and incorporation of climate velocity in biodiversity conservation, and that the emerging approaches we highlight will help generate positive long-term conservation outcomes. We also hope that the *vocc* R package we have made freely available on GitHub (https://github.com/cbrown5/vocc) for calculating local climate velocity (in conjunction with the the R code from Hamann *et al.* [28] for calculating climate-analogue velocity) will make the use of climate velocity more accessible, and thus stimulate further applications, especially by conservation practitioners.

Acknowledgments

I.B.M. is supported by the Advanced Human Capital Program of the Chilean National Commission for Scientific and Technological Research (CONICYT N° 72170231). D.S.S. is supported by Australian Research Council Discovery Grant DP170101722. A.J.R. is supported by Australian Research Council Discovery Grant DP150102656. J.G.M. is supported by the 'Tenure-Track System Promotion Program' of the Japanese Ministry of Education, Culture, Sports, Science and Technology (MEXT). C.J.B. was supported by a Discovery Early Career Researcher Award (DE160101207) from the Australian Research Council. We also thank three anonymous reviewers for constructive comments on an earlier draft of the manuscript.

References

1. Thomas, C.D. et al. (2004) Extinction risk from climate change. Nature 427 (6970), 145-148.
2. Pecl, G.T. et al. (2017) Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. Science 355 (6332).
3. IPCC, Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change., in: Meyer, R.K.P.a.L.A. (Ed.) IPCC, 2014, p. 151 pp.
4. Bellard, C. et al. (2012) Impacts of climate change on the future of biodiversity. Ecol. Lett. 15 (4), 365-77.
5. Scheffers, B. et al. (2016) The broad footprint of climate change from genes to biomes to people. Science 354 (6313).
6. Parmesan, C. (2006) Ecological and Evolutionary Responses to Recent Climate Change. Annu. Rev. Ecol. Evol. Syst. 37, 637.
7. Poloczanska, E.S. et al. (2013) Global imprint of climate change on marine life. Nat. Clim. Chang. 3 (10), 919-925.
8. Pacifici, M. et al. (2017) Species' traits influenced their response to recent climate change. Nat. Clim. Chang. 7 (3), 205-208.
9. Sandel, B. et al. (2011) The influence of Late Quaternary climate-change velocity on species endemism. Science 334 (6056), 660-4.
10. Giesecke, T. et al. (2017) Patterns and dynamics of European vegetation change over the last 15,000 years. J. Biogeogr. 44 (7), 1441-1456.
11. Dawson, T. et al. (2011) Beyond Predictions: Biodiversity Conservation in a Changing Climate. Science 332 (6025), 53-58.
12. Costello, M.J. et al. (2010) A Census of Marine Biodiversity Knowledge, Resources, and Future Challenges. PLoS One 5 (8), e12110.
13. Alberts, B. (2012) The End of "Small Science"? Science 337 (6102), 1583-1583.
14. Richardson, A.J. (2008) In hot water: zooplankton and climate change. ICES J. Mar. Sci. 65 (3), 279-295.

15. Heron, S.F. et al. (2016) Warming Trends and Bleaching Stress of the World's Coral Reefs 1985–2012. Sci. Rep. 6, 38402.
16. Loarie, S.R. et al. (2009) The velocity of climate change. Nature 462 (7276), 1052-5.
17. Ackerly, D.D. et al. (2010) The geography of climate change: implications for conservation biogeography. Divers. Distributions. 16 (3), 476-487.
18. Burrows, M.T. et al. (2011) The pace of shifting climate in marine and terrestrial ecosystems. Science 334 (6056), 652-5.
19. Garcia, R. et al., Multiple Dimensions of Climate Change and Their Implications for Biodiversity, Science, 2014, pp. 486-+.
20. Pinsky, M.L. et al. (2013) Marine taxa track local climate velocities. Science 341 (6151), 1239-42.
21. Hiddink, J.G. et al. (2015) Temperature tracking by North Sea benthic invertebrates in response to climate change. Glob. Chang. Biol. 21 (1), 117-29.
22. VanDerWal, J. et al. (2013) Focus on poleward shifts in species' distribution underestimates the fingerprint of climate change. Nat. Clim. Chang. 3 (3), 239-243.
23. Chen, Y. (2015) New climate velocity algorithm is nearly equivalent to simple species distribution modeling methods. Glob. Chang. Biol. 21 (8), 2832-2833.
24. Burrows, M.T. et al. (2014) Geographical limits to species-range shifts are suggested by climate velocity. Nature 507 (7493), 492-5.
25. Ferrier, S. et al. (2012) Queensland's biodiversity under climate change: Ecological scaling of terrestrial environmental change. CSIRO Climate Adaptation Flagship Working Paper No. 12B.
26. Ordonez, A. and Williams, J.W. (2013) Projected climate reshuffling based on multivariate climate-availability, climate-analog, and climate-velocity analyses: implications for community disaggregation. Clim. Change 119 (3-4), 659-675.
27. Williams, J.W. et al. (2007) Projected distributions of novel and disappearing climates by 2100 AD. Proc. Natl. Acad. Sci. U.S.A. 104 (14), 5738-42.
28. Hamann, A. et al. (2015) Velocity of climate change algorithms for guiding conservation and management. Glob. Chang. Biol. 21 (2), 997-1004.
29. Dobrowski, S.Z. and Parks, S.A. (2016) Climate change velocity underestimates climate change exposure in mountainous regions. Nat. Commun. 7, 12349.
30. Ordonez, A. et al. (2016) Mapping climatic mechanisms likely to favour the emergence of novel communities. Nat. Clim. Chang. 6 (12), 1104-1109.
31. Huang, M. et al. (2017) Velocity of change in vegetation productivity over northern high latitudes. Nat. Ecol. Evol. 1 (11), 1649-1654.
32. Dobrowski, S.Z. et al. (2013) The climate velocity of the contiguous United States during the 20th century. Glob. Chang. Biol. 19 (1), 241-51.
33. García Molinos, J. et al. (2016) Climate velocity and the future global redistribution of marine biodiversity. Nat. Clim. Chang. 6 (1), 83-88.
34. Barber, Q.E. et al. (2016) Assessing the vulnerability of rare plants using climate change velocity, habitat connectivity, and dispersal ability: a case study in Alberta, Canada. Reg. Environ. Change 16 (5), 1433-1441.
35. Mora, C. et al. (2013) The projected timing of climate departure from recent variability. Nature 502, 183.
36. Chen, Y. et al. (2017) Assessing the effectiveness of China's protected areas to conserve current and future amphibian diversity. Divers. Distributions. 23 (2), 146-157.
37. Carroll, C. et al. (2017) Scale-dependent complementarity of climatic velocity and environmental diversity for identifying priority areas for conservation under climate change. Glob. Chang. Biol. 23 (11), 4508-4520.
38. Harrison, S. and Noss, R. (2017) Endemism hotspots are linked to stable climatic refugia. Ann. Bot. 119 (2), 207-214.
39. Abellán, P. and Svenning, J.-C. (2014) Refugia within refugia – patterns in endemism and genetic divergence are linked to Late Quaternary climate stability in the Iberian Peninsula. Biol. J. Linnean. Soc. 113 (1), 13-28.

40. Dalsgaard, B. et al. (2014) Determinants of bird species richness, endemism, and island network roles in Wallacea and the West Indies: is geography sufficient or does current and historical climate matter? Ecol. Evol. 4 (20), 4019-31.

41. Dalsgaard, B. et al. (2011) Specialization in plant-hummingbird networks is associated with species richness, contemporary precipitation and quaternary climate-change velocity. PLoS One 6 (10), e25891.

42. Qiu, C. et al. (2014) How does contemporary climate versus climate change velocity affect endemic plant species richness in China? Chin. Sci. Bull. 59 (34), 4660-4667.

43. Roberts, D.R. and Hamann, A. (2016) Climate refugia and migration requirements in complex landscapes. Ecography 39 (12), 1238-1246.

44. Isaak, D.J. et al. (2016) Slow climate velocities of mountain streams portend their role as refugia for cold-water biodiversity. Proc. Natl. Acad. Sci. U.S.A. 113 (16), 4374-4379.

45. Fossheim, M. et al. (2015) Recent warming leads to a rapid borealization of fish communities in the Arctic. Nat. Clim. Chang. 5 (7), 673-677.

46. Sunday, J.M. et al. (2015) Species traits and climate velocity explain geographic range shifts in an ocean-warming hotspot. Ecol. Lett. 18 (9), 944-53.

47. Brown, C.J. et al. (2016) Ecological and methodological drivers of species' distribution and phenology responses to climate change. Glob. Chang. Biol. 22 (4), 1548-1560.

48. Chen, I.C. et al. (2011) Rapid Range Shifts of Species Associated with High Levels of Climate Warming. Science 333 (6045), 1024-1026.

49. Ordonez, A. et al. (2014) Combined speeds of climate and land-use change of the conterminous US until 2050. Nat. Clim. Chang. 4 (9), 811-816.

50. García Molinos, J. et al. (2017) Improving the interpretability of climate landscape metrics: an ecological risk analysis of Japan's Marine Protected Areas. Glob. Chang. Biol. 23 (10), 4440-4452.

51. Batt, R.D. et al. (2017) Gradual changes in range size accompany long-term trends in species richness. Ecol. Lett. 20 (9), 1148-1157.

52. Magurran, A.E. et al. (2015) Rapid biotic homogenization of marine fish assemblages. Nat. Commun. 6, 8405.

53. Bertrand, R. et al. (2011) Changes in plant community composition lag behind climate warming in lowland forests. Nature 479 (7374), 517-20.

54. Devictor, V. et al. (2012) Differences in the climatic debts of birds and butterflies at a continental scale. Nat. Clim. Chang. 2 (2), 121.

55. Hiddink, J.G. et al. (2012) Keeping pace with climate change: what can we learn from the spread of Lessepsian migrants? Glob. Chang. Biol. 18 (7), 2161-2172.

56. Schloss, C.A. et al. (2012) Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. Proc. Natl. Acad. Sci. U.S.A. 109 (22), 8606-8611.

57. Corlett, R.T. and Westcott, D.A. (2013) Will plant movements keep up with climate change? Trends Ecol. Evol. 28 (8), 482-8.

58. Lindström, Å. et al. (2013) Rapid changes in bird community composition at multiple temporal and spatial scales in response to recent climate change. Ecography 36 (3), 313-322.

59. Hulme, P.E. (2014) Alien plants confront expectations of climate change impacts. Trends Plant. Sci. 19 (9), 547-9.

60. Chivers, W.J. et al. (2017) Mismatch between marine plankton range movements and the velocity of climate change. Nat. Commun. 8, 14434.

61. García Molinos, J. et al. (2017) Ocean currents modify the coupling between climate change and biogeographical shifts. Sci. Rep. 7 (1), 1332.

62. HilleRisLambers, J. et al. (2013) How will biotic interactions influence climate change-induced range shifts? Ann. N. Y. Acad. Sci. 1297, 112-25.

63. Tingley, M.W. et al. (2014) Fine- and coarse-filter conservation strategies in a time of climate change. Ann. N. Y. Acad. Sci. 1322, 92-109.

64. Lenoir, J. and Svenning, J.C. (2015) Climate-related range shifts - a global multidimensional synthesis and new research directions. Ecography 38 (1), 15-28.

65. McGuire, J.L. et al. (2016) Achieving climate connectivity in a fragmented landscape. Proc. Natl. Acad. Sci. U.S.A. 113 (26), 7195-7200.
66. Saerens, M. et al. (2009) Randomized Shortest-Path Problems: Two Related Models. Neural Comput. 21 (8), 2363-2404.
67. Carroll, C. et al. (2015) Biotic and Climatic Velocity Identify Contrasting Areas of Vulnerability to Climate Change. PLoS One 10 (10), e0140486.
68. Zheng, B. et al. (2016) Velocity of temperature and flowering time in wheat – assisting breeders to keep pace with climate change. Glob. Chang. Biol. 22 (2), 921-933.
69. Hampe, A. and Jump, A.S. (2011) Climate Relicts: Past, Present, Future. Annu. Rev. Ecol. Evol. Syst. 42 (1), 313-333.
70. Halpern, B.S. et al. (2010) Placing marine protected areas onto the ecosystem-based management seascape. Proc. Natl. Acad. Sci. U.S.A. 107 (43), 18312-18317.
71. Wells, S. et al. (2016) Building the future of MPAs – lessons from history. Aquat. Conserv. Mar. Freshw. Ecosyst. 26, 101-125.
72. Hannah, L. (2008) Protected Areas and Climate Change. Ann. N. Y. Acad. Sci. 1134 (1), 201-212.
73. Batllori, E. et al. (2017) Potential relocation of climatic environments suggests high rates of climate displacement within the North American protection network. Glob. Chang. Biol. 23 (8), 3219-3230.
74. Venter, O. et al. (2017) Bias in protected-area location and its effects on long-term aspirations of biodiversity conventions. Conserv. Biol. DOI: 10.1111/cobi.12970.
75. Pressey, R.L. et al. (2017) From displacement activities to evidence-informed decisions in conservation. Biol. Conserv. 212 (Part A), 337-348.
76. Fogarty, H.E. et al. (2017) Are fish outside their usual ranges early indicators of climate-driven range shifts? Glob. Chang. Biol. 23 (5), 2047-2057.
77. Sen Gupta, A. et al. (2015) Episodic and non-uniform shifts of thermal habitats in a warming ocean. Deep. Sea. Res. Part 2 113, 59-72.
78. Venegas-Li, R. et al. (2017) 3D spatial conservation prioritisation: Accounting for depth in marine environments. Methods Ecol. Evo. DOI: 10.1111/2041-210X.12896.
79. Levin, N. et al. (2017) Adding the Third Dimension to Marine Conservation. Conserv. Lett. DOI: 10.1111/conl.12408.
80. Llovel, W. et al. (2014) Deep-ocean contribution to sea level and energy budget not detectable over the past decade. Nat. Clim. Chang. 4 (11), 1031-1035.
81. Roberts, C.M. et al. (2017) Marine reserves can mitigate and promote adaptation to climate change. Proc. Natl. Acad. Sci. U.S.A. 114 (24), 6167-6175.
82. Clark, M.R. et al. (2010) The ecology of seamounts: structure, function, and human impacts. Ann. Rev. Mar. Sci. 2, 253.
83. Morato, T. et al. (2010) Seamounts are hotspots of pelagic biodiversity in the open ocean. Proc. Natl. Acad. Sci. U.S.A. 107 (21), 9707-9711.
84. Stramma, L. et al. (2010) Ocean oxygen minima expansions and their biological impacts. Deep. Sea. Res. Part 1 Oceanogr. Res. Pap. 57 (4), 587-595.
85. Thomas, C.D. (2011) Translocation of species, climate change, and the end of trying to recreate past ecological communities. Trends Ecol. Evol. 26 (5), 216-221.
86. Ordonez, A. and Williams, J.W. (2013) Climatic and biotic velocities for woody taxa distributions over the last 16 000 years in eastern North America. Ecol. Lett. 16 (6), 773-81.
87. Serra-Diaz, J.M. et al. (2014) Bioclimatic velocity: the pace of species exposure to climate change. Divers. Distributions. 20 (2), 169-180.
88. Comte, L. and Grenouillet, G. (2013) Do stream fish track climate change? Assessing distribution shifts in recent decades. Ecography 36 (11), 1236-1246.
89. Ohlemüller, R. (2011) Running Out of Climate Space. Science 334 (6056), 613-614.
90. Schliep, E. et al. (2015) Stochastic Modeling for Velocity of Climate Change. J. Agric. Biol. Environ. Stat. 20 (3), 323-342.
91. Gaines, S. et al. (2007) Connecting Places: The Ecological Consequences of Dispersal in the sea. Oceanography 20 (3).

92. Cowen, R. et al. (2007) Population Connectivity in Marine Systems: An Overview. Oceanography 20 (3), 14-21.
93. Belanger, C.L. et al. (2012) Global environmental predictors of benthic marine biogeographic structure. Proc. Natl. Acad. Sci. U.S.A. 109 (35), 14046-14051.
94. Moss, R. et al., Towards New Scenarios for Analysis of Emissions, Climate Change, Impacts, and Response Strategies, Intergovernmental Panel on Climate Change, Geneva, 2008, p. 132.
95. Sol, D. et al. (2012) Unraveling the Life History of Successful Invaders. Science 337 (6094), 580-583.

Figures

Figure 1. Mathematical and graphical differences between (A) local climate and (B) climate-analogue velocities.

Figure 2. Tailoring climate velocity to be more biologically meaningful. (A) The local velocity associated with a cell in flat terrain (black square - L_1), typically high because of the relatively flat spatial thermal gradient (note the widely spaced isotherms), can overestimate true migration requirements by only considering the immediate surroundings (a 3x3 neighbourhood in this case) if suitable future habitats are nearby (grey square). Conversely, in mountainous terrain (red square - L_2), steep gradients resulting in low climate velocity can underestimate migration requirements where no suitable habitat (orange square) is available in the surroundings (e.g., locations close to mountain tops), despite the perceived low migration requirements. (B) Where human-assisted migration is not of concern and the purpose is to infer potential biological responses, climate-analogue velocities can be too inclusive by searching for future climate analogues (orange squares) across unrealistically wide regions beyond the distances species might be able to disperse over time (inner circle – tree, outer circle – bird). (C) Thresholds can be set by reference to the thermal tolerances of representative taxa (upper row) or the local historical climate variability (lower row) characterizing the range of climatic conditions local populations are adapted to (grey box bounding the extremes of the local temperature time series for a reference period). Future mean thermal conditions at the focal cell L_2 (dotted red line, first column) move beyond the upper thermal tolerance of the species and outside the bounds of historical local thermal variability, suggesting a likely extirpation of the local population. On the other hand, the two candidate target sites (L_3, L_4) within the dispersal range will develop analogue climates for the species as their future thermal environments will be within the threshold (note that L_4 will be a climate analogue only under one criterion). The selected target locality for the calculation of the analogue velocity would be the geographically closest climate analogue to the focal cell (L_3). Alternatively, cost-path analysis could be used instead of Euclidean

distances to reflect more realistically the influence of thermal gradients (climate connectivity) and other non-climate factors on the dispersal route between present and future analogues.

Elements

Glossary

BOX 1. The ecological context of climate velocity

BOX 2. Caveats associated with climate velocity

BOX 3. Methodological considerations when applying climate velocity

BOX 4. A case study applying climate velocity, residence time and climate-velocity trajectories to the UK marine protected area network

SI – Additional support figures and tables

Glossary

Bioclimatic or biotic velocity: Based on data from species' range shifts using climate maps of suitable and unsuitable areas, biotic velocity estimates the rate at which species must move to track their climate niche. For any species, it is calculated as the distance between a site and the nearest location considered to be suitable for that species within its future projected range [67, 86]. Biotic velocity has also been termed bioclimatic velocity [87], and calculated following the local climate velocity approach using species' suitability maps instead of climate maps to obtain temporal trends and spatial gradients. Sometimes a distinction is made between these terms based on whether ranges and habitat suitability for the periods being analysed are projected or predicted [88].

Climate-analogue velocity: A climate-velocity metric that considers the distance between points at a particular point in time and their future climate analogues, divided by the time difference (Fig. 1B). There are two types: *forward analogue velocity*, which is the straight-line speed and direction required to reach a given climate-analogue destination at some point in the future (usually a single destination for any origin under consideration); and *backward analogue velocity*, which considers a destination and asks which points (usually several) of origin might eventually feed into the destination.

Climate residence time: The amount of time necessary for a climate isoline to emerge from a specific area (usually a protected area). It is estimated as the (equivalent) diameter of the area divided by the mean climate velocity within that area [16].

Isoline: A line connecting points of equal value across space. Isoline, isocline, and isopleth are all synonyms.

Local climate velocity: The original climate-velocity metric [16] that has two main components in its calculation: a temporal trend and a spatial gradient, both for the same climate variable (Fig. 1A). Local climate velocity is an estimate of the instantaneous climate velocity of an isoline at a location.

Box 1. The ecological context of climate velocity

Estimates of speed and direction associated with climate velocity can be conceptualized by considering air temperature on land. Because air temperature decreases predictably with elevation (~6.5°C per 1,000 m), as the climate warms, an organism at the bottom of a hill tends to move uphill or to the nearest climate-analogue area to maintain its thermal environment (i.e., short-distance dispersal). This would yield slow (low) climate velocities (directed uphill or to the closest climate analogue area), because an organism does not need to move far to maintain its thermal environment (Figure I blue arrow). Conversely, flat landscapes are more homogenous thermal environments, and an organism experiencing a warming landscape might need to migrate a long way to remain in its original thermal environment (i.e., long-distance dispersal). This would manifest as a high climate velocity directed towards the nearest occurrence of the original temperature (Figure I red arrow).

Figure I. Understanding climate velocity on land.

How the distribution of a species responds to a gradual change in its climate space [89] requires consideration of the relationship between a species' physiological tolerance and range dynamics. This can be conceptualized in two ways: a representation of a species' performance curve across a latitudinal gradient (Figure IIA), and a geographical representation of species' distribution across a latitudinal gradient (Figure IIB). As climate warms, the initial location of the thermal performance curve will shift in space towards cooler environments, commonly higher latitudes (Fig. IIA). This shift in climate, which can be represented by climate velocity, will tend to cause geographic range shifts in species' distribution (i.e., range expansions or contractions of local populations), as species maintain their original thermal environment (Fig. IIB).

Figure II. (A) Simple bell-shaped curve for the relationship between species distribution and performance (probability of occurrence) across a latitudinal gradient under climate change.

(B) The distribution of a species showing separate populations (dark circles) across a latitudinal gradient at two times. Local population contractions and expansions are observed at each range edge at time *t2*.

Box 2. Caveats associated with climate velocity

Climate velocity is not species movement. When discussing climate velocity, it is sometimes easy to fall into the trap of making unsupported claims about species movement. A range-edge might be more likely to move if it is near the species' thermal maximum, but other responses to climate change are possible, including behavioural modification and genetic selection, which are more important in species with limited capacity to disperse.

The fractional nature of the local climate velocity metric can be misleading. Because local climate velocity is the ratio of the temporal trend over the spatial gradient in climate, small and biologically irrelevant temporal trends over vanishingly small spatial gradients can lead to high local climate velocities. Imagine two different locations on the Earth's surface, one of which warms by 0.1°C over a given time, and the other by 1°C over the corresponding period. Further imagine that tracking the 0.1°C change experienced at the first location requires moving 100 km, while tracking the 1°C change at the second location requires moving 50 km. The first location has twice the climate velocity of the second, but it ignores the magnitude of change at the location itself, which can sometimes be a better index of the need for a range shift.

Climate velocity currently has no standard measure of uncertainty. There are many potential sources of uncertainty in estimates of climate velocity that are usually unacknowledged. These include (but are not limited to): (a) error in the gridded climate metrics that affect estimates of spatial gradient and temporal trend in the climate variable, and (b) variability both within individual climate projections (model runs) and among climate projections (different general circulation models and representative concentration pathways). Schliep *et al.* [90] go beyond the conventional finite-difference approach to climate velocity explained here by modelling temperature (as an example of a climate variable) as a function of both space and time within a stochastic Bayesian framework. This allows the quantification of variability associated with simultaneous estimates of spatial gradients and temporal trends in temperature (i.e., uncertainty source (a) above). Although this process is numerically complex and computationally demanding, it is an important first step in quantifying uncertainty. Accounting for remaining sources of uncertainty require further research.

Climate velocity does not include biological information. In its simplest form, climate velocity does not include biological information such as dispersal potential of species, landscape permeability, habitat suitability, or species interactions. This lack of biological information means that climate velocities are general; any increase in biological realism reduces this generality (see Section *1. Tailoring climate velocity to be more biologically meaningful*).

Box 3. Methodological considerations when applying climate velocity

Which environmental variables?

Most analyses of climate velocity have used temperature, as it influences species' distributions on land, in freshwater, and in the ocean. Temperature is a particularly strong environmental driver in the ocean because it is correlated with nutrient availability, thereby also controlling system structure and function [14]. But climate velocity can be applied to any environmental variable. For example, on land, climate-velocity analyses have often included rainfall because the distribution and productivity of plant communities is regulated by water availability.

When applying climate velocity to a new environmental variable, one should consider the functional relationship between the environmental driver and its biological response. Climate velocity might have ecological relevance for a variable where the relationship with biological performance is symmetrical (Box 1), but might not if it is a step function. For example, most marine life cannot survive oxygen concentrations <2 mg.l^{-1}, and tracking this "threshold" oxygen isoline might be more informative than estimating climate velocity for all isotherms, most of which are not ecologically relevant. Technically this is just the analogue velocity of a single isoline.

Finally, most environmental variables are represented in climate-velocity analyses using summary statistics, and their selection warrants careful consideration. For example, annual mean values might better predict shifts over the entire species' ranges, while extreme values might be more appropriate at range edges. Similarly, bottom temperatures are more appropriate than surface temperatures for bottom-dwelling marine species [21]. The often unacknowledged uncertainties associated with data products should also be considered (Box 2).

What time scales?

Climate velocity is best suited to studies of climate-change impacts, which by definition, implies time scales of decades or longer.

What space scales?

Climate velocity has been applied to gridded environmental data at spatial scales from ~1 km to ~110 km. On land, most applications have used a fine spatial resolution (e.g., a few kilometres [26], [32]), reflecting the importance of terrain on microclimates and organism dispersal [29]. By contrast, analyses in the ocean have used a coarser spatial resolution (e.g., a hundred kilometres), not only because fine-scale data are not always available, but because there are fewer dispersal barriers [91] so organisms disperse further, and because microclimates might be less important [92]. However, shallow-water and seafloor communities are structured more by biological than environmental processes [93], suggesting the need for finer-scale analyses. It might be desirable in some instances to match the spatial resolution to climate turnover, so that the spatial resolution might be finer around mountains than plains, and coastally than in the open ocean. Irrespective, coarser spatial resolution leads to greater climate velocity because it averages over fine-scale variation [32].

Combining environmental variables?

Climate velocity has usually been applied to an individual variable. When considering multiple variables (e.g., temperature and rainfall), these have generally been treated separately as independent drivers of species movement [17, 26, 32]. However, Hamann *et al.* [28] developed a multivariate approach to climate-analogue velocity based on a Principal Components Analysis of multiple metrics (e.g., minimum, maximum, mean) of temperature and rainfall. This approach has the benefit of considering the multivariate movement of climate space, but at the cost of complicating interpretation. Moreover, multivariate climate-analogue velocities are likely to be higher than corresponding univariate estimates [28, 34], since finding similar multivariate climates will often require a large search radius (i.e., similar rainfall is likely to be found closer than similar rainfall and temperature combined). The magnitude of this effect can be mitigated by relaxing assumptions defining analogue climates (e.g., expanding bandwidth to incorporate more climate variability [67]). Multivariate local climate velocity could be calculated by applying vector algebra to multiple univariate estimates of local climate velocity. For example, if there were two univariate climate velocities (e.g., temperature and rainfall) in opposing directions and equal in magnitude they would cancel. However, in general, the new multivariate climate space would not be the same as the original. This divergence in angles of such univariate estimates can be considered as a measure of climate stress on an organism and has provided insight into potential ecological responses to multivariate climate change [30].

Box 4. A case study applying climate velocity, residence time and climate-velocity trajectories to the UK marine protected area network

To illustrate the utility of climate velocity to networks of marine protected areas (MPA), we examine climate conditions across the network in UK territorial waters for past (1960-2009) and future (2006-2050) climate at 1° spatial resolution. Past and future local climate velocities were calculated, respectively, from annual mean sea surface temperatures (SSTs) from the Hadley Centre data set HadISST 1.1 and a multi-model ensemble for the IPCC RCP8.5 climate pathway [94]. Climate velocities were calculated for both periods as cell ratios of the local temporal trend (slope from the linear regression of annual SST over time) to the (3x3) spatial gradient based on average annual mean SSTs [18]. Local climate velocity associated with the MPA network over the past 50 years in UK waters shows strong contrasts between western and eastern halves of the UK Exclusive Economic Zone (Figure IA). However, both sides are projected to have similar magnitudes of local climate velocity by 2050, because of a general decrease in local climate velocity in the North Sea and local increases on the western side (Figure IB). The large spatial variability in local climate velocity will require species responding to climate change to shift their distribution up to 10 times faster or slower depending on the location of the MPA within the network.

On the other hand, climate residence time shows high variation across the UK MPA network for both periods (Figure IC,D). MPAs along the west coast of Scotland are predicted to register largest reductions in residence time, while those within the Irish Sea and north of the Strait of Dover are predicted to increase. Reduction of residence time suggests reduced viability of a protected area as the rate of change in conditions within the area increases, potentially compromising local adaptation to climate change, especially of range-restricted species, while facilitating the establishment of immigrant and invasive species [95].

Climate-velocity trajectories over the past 50 years are generally directed poleward along the English coast (Figure IE), suggesting that the coastal network currently exhibits good connectivity (MPAs in the north should receive climate migrants from those in the south as temperature warms). However, climate-velocity trajectories until 2050, as projected from RCP8.5, show a different pattern on the east coast of the UK, where thermal niches move offshore into the North Sea towards Scandinavia (Figure IF). This scenario suggests that littoral species on this coast might be forced to adapt *in situ*, because they become disconnected from their current thermal niches. This could have management implications, especially for smaller protected areas on the east coast of Scotland, where residence times will continue to be short. Here, the possibility of assisted migration and translocations of species of concern might be considered.

Figure I. A case study illustrating the application of (A, B) local climate velocity, (C, D) residence time, and (E, F) climate trajectories. (A, C, E) past (1960-2009) and (B, D, F) future (2006-2050) climate conditions across the MPA network in UK territorial waters (dashed line). For each MPA centroid (points on the maps), we show the expected thermal shift by projecting its SST in time following the speed and direction of local climate velocities (VoCC) at each cell.

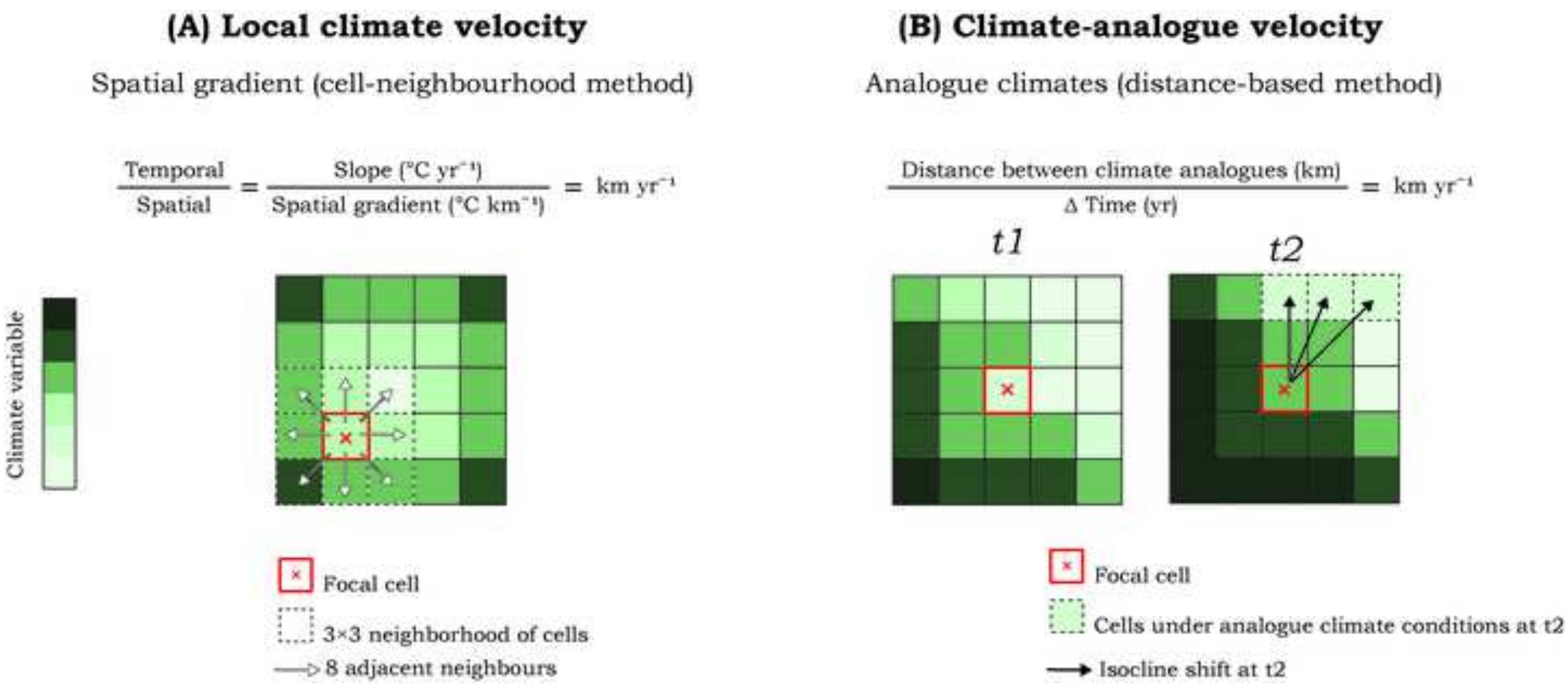
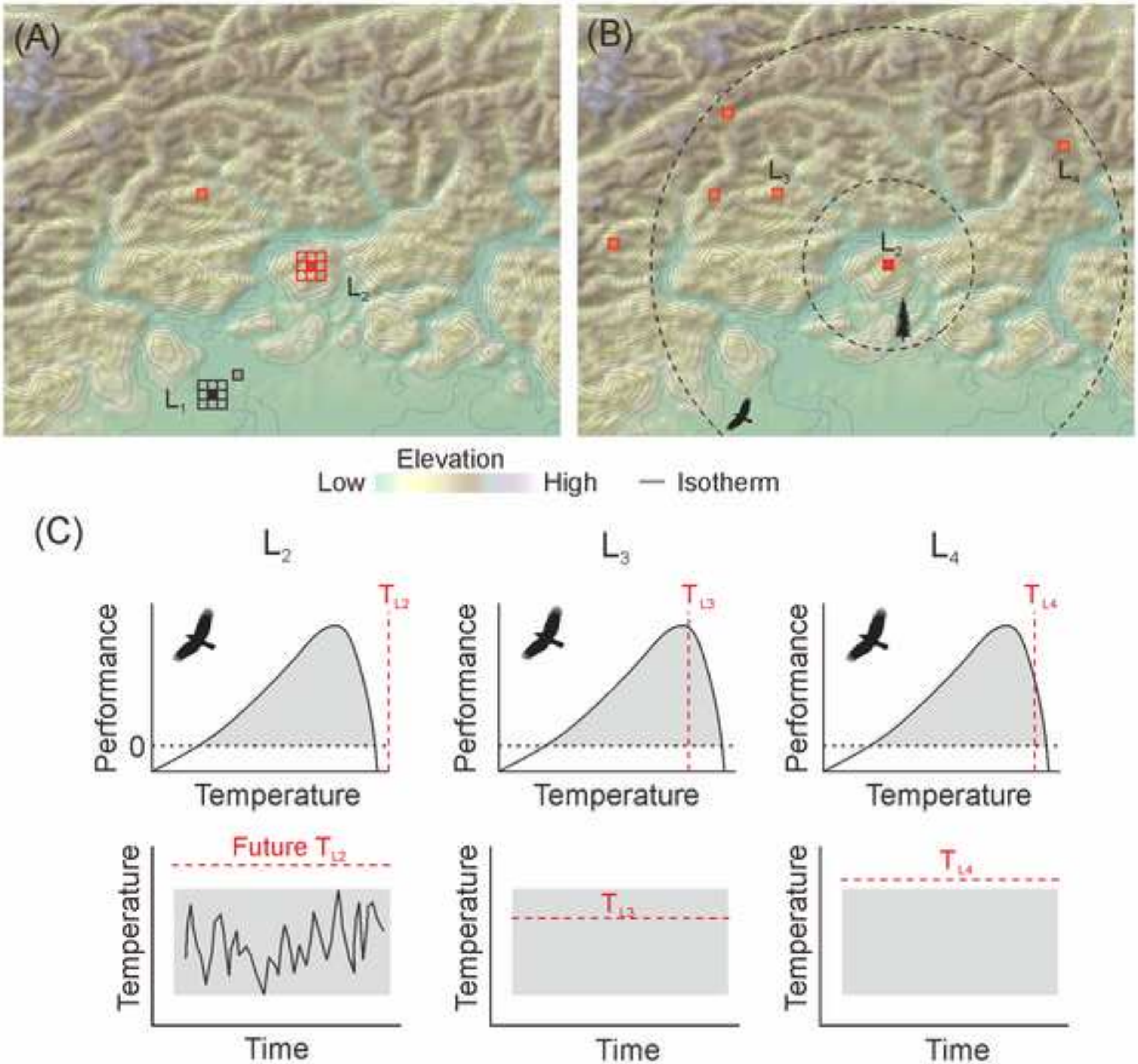

(A) Local climate velocity
Spatial gradient (cell-neighbourhood method)
Temporal / Spatial = Slope (°C yr⁻¹) / Spatial gradient (°C km⁻¹) = km yr⁻¹
Climate variable
Focal cell
3×3 neighborhood of cells
8 adjacent neighbours
(B) Climate-analogue velocity
Analogue climates (distance-based method)
Distance between climate analogues (km) / Δ Time (yr) = km yr⁻¹
t1
t2
Focal cell
Cells under analogue climate conditions at t2
Isocline shift at t2

Figure 2

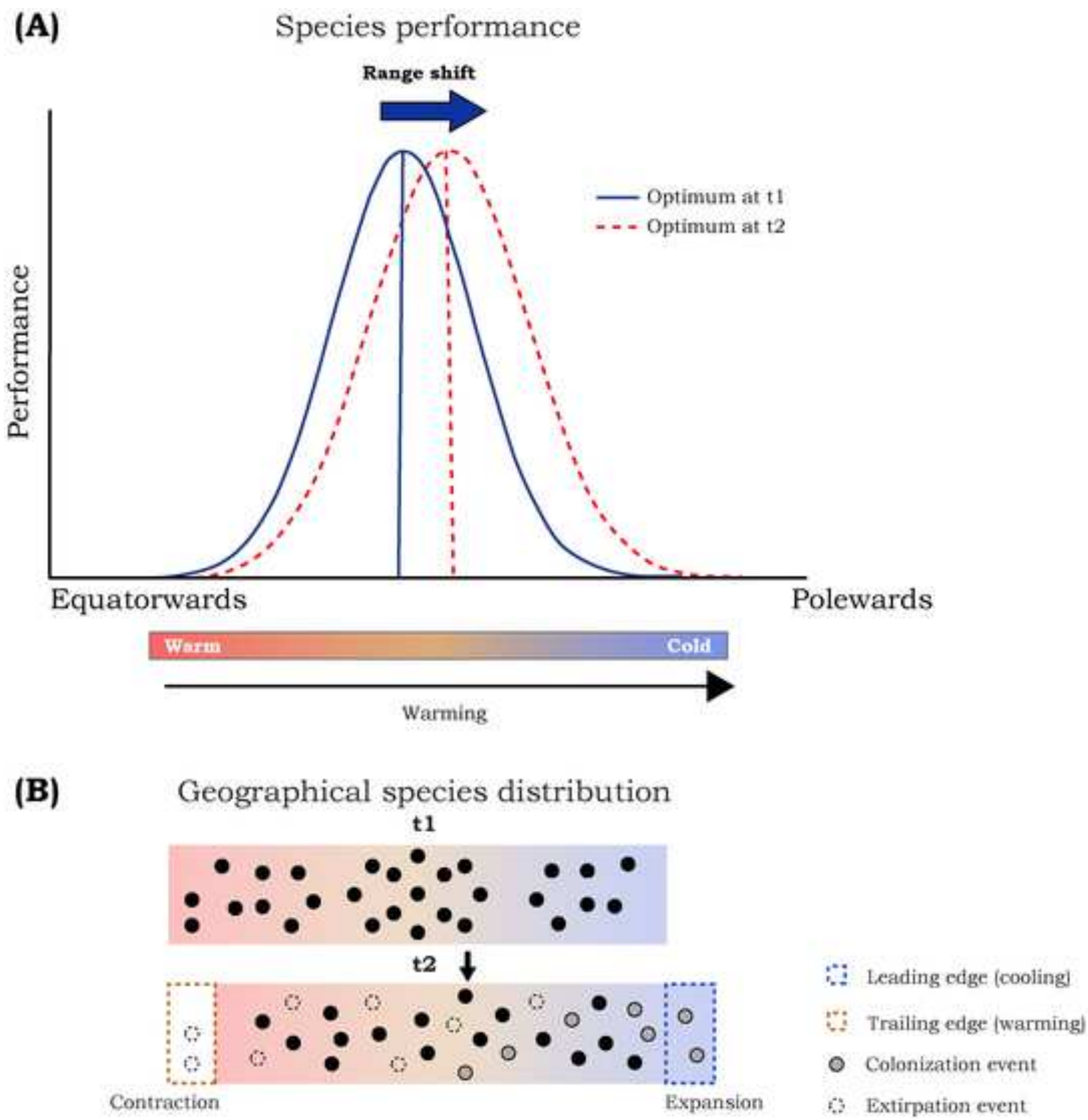


(A)
L1
L2
(B)
L3
L4
L2
Elevation
Low
High
Isotherm
(C)
L2
L3
L4
TL2
TL3
TL4
Performance
0
Temperature
Future TL2
TL3
TL4
Temperature
Time

Box 1 Figure I

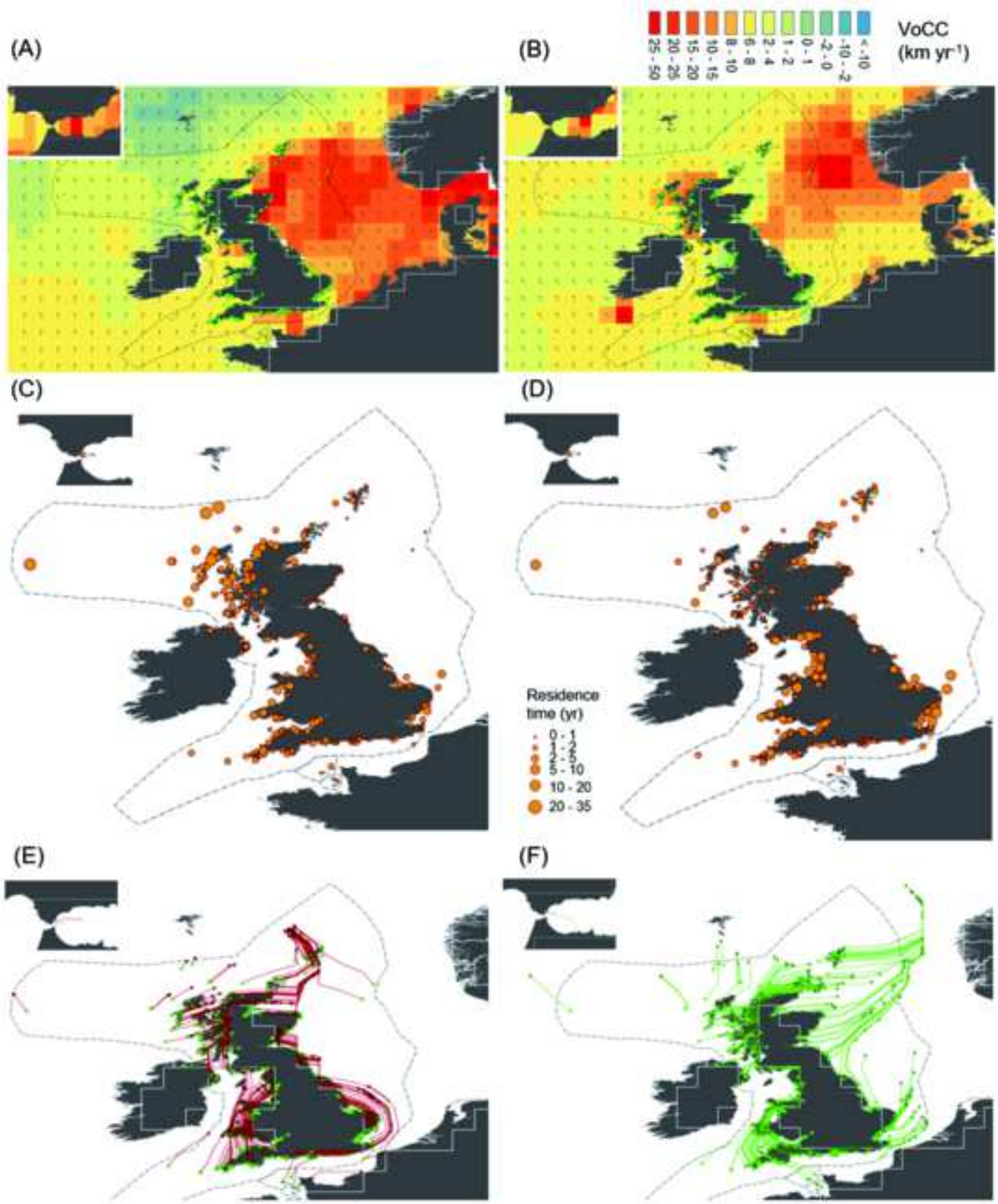
Box 1 Figure II

Click here to download Figure Box1FigureII.jpg



Box 4 Figure I

Click here to download Figure Box4FigureI.tif



Outstanding Questions:

We dropped this section out according with author instructions

Figure 1

Box 1 Figure I

Click here to access/download
Original Figure File
Box1FigureI.ai

Box 1 Figure II

Click here to access/download
Original Figure File
Box1FigureII.ai