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### *Climate Velocity Can Inform Conservation in a Warming World*

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# 1 **Climate velocity can inform conservation in a warming world**

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37  
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39 biodiversity

40  
41 **Abstract**

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

52

### 53 **Simple climate metrics could help conservation in a changing climate**

54 Climate change is likely to become the most serious threat to biodiversity this century [1, 2].  
55 In fact, anthropogenic climate change, initiated in the Industrial Revolution, has already  
56 affected ecological systems from individual organisms to biomes [3, 4], and has influenced  
57 >80% of all biological processes [5]. Although ecological responses to climate change are  
58 numerous, complex and multi-faceted, probably the most fundamental is the spatial  
59 redistribution of global biodiversity [3]. Such species range shifts, in response to a changing  
60 climate, have been observed across terrestrial and marine ecosystems during the current  
61 warming period [6-8] and since the last glacial maximum [9, 10]. Understanding the  
62 processes underpinning range shifts and predicting their potential outcomes is needed to  
63 inform conservation, and reduce risks to food security, human health, and the viability of  
64 numerous industries that depend on ecosystem services, including forestry, fisheries, and  
65 eco-tourism.

66  
67 Mechanisms underpinning range shifts are a blend of a species' exposure, sensitivity and  
68 vulnerability to climate change, combined with its adaptive capacity [11]. Of these  
69 characteristics, only exposure to climate change might be considered relatively generic  
70 across species, with other traits being specific to individual species or populations. But  
71 detailed physiological, ecological and evolutionary data are missing for most species,  
72 especially in the tropics and much of the global ocean [12], and current research priorities  
73 make collection of such data increasingly difficult [13, 14]. This leaves conservation and  
74 management agencies to make decisions with whatever alternative tools are available.  
75 Threats to biodiversity posed by climate change have thus traditionally been quantified using  
76 rates of warming or cooling, temperature anomalies, or degree heating weeks [15]. What  
77 these simple indices do not convey is the relative likelihood that a species might escape the  
78 threat of climate change by shifting its distribution. A promising solution that retains  
79 generality, but conveys more ecologically relevant information is the velocity of climate  
80 change, or more simply, climate velocity [16-18]. Climate velocity is a metric that uses freely-

81 accessible environmental and climate data, without the need for detailed ecological  
82 knowledge [19], to approximate the observed shifts in species' distributions [20-23]. Climate  
83 velocity thereby provides a simple and intuitive measure of threats to biodiversity posed by  
84 climate change [24] and as such, in its simplest form, is not bespoke for particular species.

85  
86 Here, we explore the meaning, utility and application of climate velocity, with a particular  
87 focus on the potential for its use to guide conservation under a changing climate. We begin  
88 by defining the concept of climate velocity, as there are several formulations with different  
89 conceptual underpinnings. This leads to a summary of the methodological aspects and  
90 caveats that need to be considered when using climate velocity. We then describe the  
91 different applications of climate velocity that have provided new insights into many areas of  
92 climate-change ecology. Next, we look to the future and explore four ways to improve the  
93 utility of climate velocity in conservation. We focus on simple metrics that use raw climate  
94 variables, and do not consider velocities that can be calculated from species distribution  
95 models or assemblage models that scale climate space by biological data (e.g., Generalized  
96 Dissimilarity Modelling) [25]. This review is targeted at ecologists seeking to understand how  
97 climate change could affect communities, and for conservation practitioners wanting to  
98 include climate change in their planning.

99

## 100 **What is climate velocity?**

101 Climate velocity is a vector that describes the speed and direction that a point on a gridded  
102 map would need to move to remain static in climate space (e.g., to maintain an isoline of a  
103 given variable in a univariate environment) under climate change (see Glossary). From an  
104 ecological perspective, climate velocity can be conceptualized as the speed and direction in  
105 which a species would need to move to maintain its current climate conditions under climate  
106 change (see Box 1). For this reason, climate velocity can be considered the potential  
107 exposure to climate change faced by a species, if the climate moves beyond the  
108 physiological tolerance of a local population. Despite the intuitive ecological relevance,

109 however, climate velocity is based solely on environmental variables and not on species  
110 data (Box 1).

111

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

126

127 Climate-analogue velocity [26] emerged as an extension of the climate analogue concept  
128 [27] – i.e., the identification of points in space with climates sufficiently similar to those of the  
129 points under consideration (Figure 1). Euclidean distances are often used as measures of  
130 multivariate climatic dissimilarity, climate analogy being set by reference to a dissimilarity  
131 threshold defined either subjectively [28, 29] or using regional statistics (e.g., 95<sup>th</sup> percentile  
132 of the minimum Euclidean distance between each future climate and all current climates)  
133 [26, 30]. Importantly, the selected threshold is constant and common to all local climates.  
134 When the points under consideration represent the current climate, and their analogues are  
135 sought in a future climate, the geographic distance between points can be divided by the  
136 time separating the periods to compute a speed of climate change. The direction for the

137 climate-analogue velocity is provided by the relative positions of the original point and its  
138 future analogue (Figure 1B). Climate-analogue velocity can be further conceptualized in two  
139 related but distinct ways: “*forward*” *analogue velocity*, the original formulation, and  
140 “*backward*” *analogue velocity*, which is the inverse of forward velocity ([28], Glossary).

141

142 Local and climate-analogue velocities have been used in different situations. Local climate  
143 velocity has usually been used for exploring potential responses of biota to single variables,  
144 usually temperature [31], but sometimes precipitation [32]. This metric has been favoured  
145 by ecologists when gradients are smooth and where there is one main variable driving  
146 change (e.g., in the open ocean, Figure S1). Local climate velocity can be constrained by  
147 species requirements for particular habitat features, such as being limited to coastal marine  
148 regions by the need for light on the sea bottom, or substratum types for reef formation, or  
149 intertidal zones [33]. By contrast, climate-analogue velocity has usually been used with  
150 multiple variables [34]. It has greater ecological realism in complex environments with  
151 contrasting climatic gradients, and is favoured by ecologists dealing with species with  
152 multiple needs. For example, on land, temperature and rainfall have often been analysed in  
153 multivariate space using climate-analogue velocity (Figure S1). Irrespective of the climate-  
154 velocity metric used and data availability, researchers should be aware of several associated  
155 caveats (Box 2), and a suite of methodological aspects, including which environmental  
156 variables to use, their time and space scales, and how to combine multiple variables (Box  
157 3).

158

159 To encourage the robust use of climate velocity in the ecological and conservation research  
160 communities, we provide two resources. The first is a collection of R functions aggregated  
161 into a package, *vocc*, that is freely available on GitHub (<https://github.com/cbrown5/vocc>).  
162 This package calculates the local climate velocity for univariate environmental datasets, on  
163 local to global scales (see the SOM of Hamann *et al.* [28] for R code for climate-analogue  
164 velocity). The second resource is a list of all freely available environmental datasets (and

165 their websites) that have been used in climate-velocity research (Table S1 supplemental  
166 online information).

167

## 168 **Current applications of climate velocity**

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

173

### 174 *1. Climate residence time*

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

190

### 191 *2. Climate refugia and rates of endemism*



192 Areas of low local climate and climate-analogue velocities can be considered candidate  
193 areas for protection [24, 37] because they are likely to contain a consistent suite of species  
194 and their ecological interactions as they evolved together in a slowly moving climate. Such  
195 areas are often called climate refugia, and have been linked with high levels of endemism  
196 [38]. For example, Sandel *et al.* [9] related local climate velocity between the last glacial  
197 maximum and current climates, and used these to explore endemism of amphibians,  
198 mammals and birds. Relationships between climate velocity and rates of endemism were  
199 weakest for wide-ranging species and strongest for narrow-ranged species, suggesting that  
200 areas of slow climate velocity provide important refugia for biodiversity under climate  
201 change. Subsequent studies on endemic species of insects and mammals [39], birds [40,  
202 41], and plants [42, 43] confirm these patterns at a regional scale, and patterns seem to  
203 hold even at local scales within freshwater streams [44].

204

### 205 3. *Historic range shifts*

206 The magnitude and direction of local climate velocity explains range shifts in many species  
207 on land [22] and in the ocean [7, 21, 22, 45-47]. For example, on land, global meta-analysis  
208 of over the past 40 years showed that terrestrial species tracked local climate velocity in  
209 response to warming to higher latitudes and higher elevation [48]. In marine systems,  
210 extensive data on marine species (128 million individual fish and invertebrate records across  
211 360 harvested species) around North America closely track local climate velocity, both  
212 horizontally and vertically in the ocean, over the past 50 years [20]. We expect greater  
213 agreement between climate velocity and species distribution shifts in homogenous systems  
214 such as the open ocean and continental plains. Such homogenous systems pose fewer  
215 constraints on movement because species are more able to follow local climate velocity,  
216 whereas heterogeneous and complex systems have barriers to dispersal and movement  
217 that can constrain distribution shifts. In such environments, estimates of climate velocity can  
218 be modified – see Section *Tailoring climate velocity to be more biologically meaningful*. Note

219 also that even in relatively homogenous regions, divergence among climate variables  
220 mediating species' distributions might complicate responses.

221

#### 222 *4. Exposure of organisms to climate change, migration velocities and the formation of novel* 223 *communities*

224 Because climate velocity quantifies the speed and direction of a changing climate, it also  
225 quantifies the exposure of a species to climate change [19, 29]. Recently, Ordonez *et al.*  
226 [30] used local climate velocity as one of three mechanisms driving the reshuffling of species  
227 and emergence of novel communities under climate change, the other two being climate  
228 novelty (opening of new suitable environments) and divergence (discrepancy in the direction  
229 of change among gradients of different climate variables in relation to a species' niche). As  
230 elsewhere [24, 26, 49], slow local and climate-analogue velocities were associated with  
231 regions of strong spatial gradients in environmental conditions (e.g., mountains) and  
232 assumed to be least-exposed to climate change (i.e., requiring shorter dispersal distances  
233 to track changes in climate). Climate exposure can also be modified by climate connectivity  
234 (see below) [24, 29, 50]. In this case, exposure relates to the cost of moving through  
235 climatically heterogeneous land- or seascapes, possibly accounting for other non-climate  
236 drivers conditioning dispersal [29].

237

#### 238 *5. Climate-velocity trajectories and climate connectivity*

239 To address Loarie *et al.*'s [16] caution that local climate velocity is discontinuous, Burrows  
240 *et al.* [24] developed climate-velocity trajectories by moving climate "tracers" between  
241 neighbouring grid cells based on the local climate velocity. Climate-velocity trajectories thus  
242 track specific climate conditions through time as continuous paths (see Box 4 Figure I).  
243 Spatially aggregated patterns of climate-velocity trajectories suggest changes in species  
244 richness with climate, and notably highlight areas that might receive few or no climate  
245 migrants through lack of connections to warmer places (climate 'sources': locally warm  
246 areas such as equatorward-facing coastlines on land or poleward-facing coastlines in the

247 ocean), and areas where there might be local extirpations through lack of connections to  
248 cooler areas (climate 'sinks': locally cool areas such as mountain tops on land and  
249 equatorward facing coastlines in the ocean) (e.g. [2, 22]).

250

## 251 6. Projected range shifts with climate change

252 As climate velocity is an indicator of the speed at which species' range shifts track climate  
253 change – potentially the maximum possible rate of range shift when dispersal is not a limiting  
254 factor – climate-driven changes in the geographical distribution of species can be simply  
255 predicted by forward (or backward) projection of their climate envelopes (see Glossary)  
256 following the speed and direction of local or analogue climate velocities. This approach has  
257 been combined with species' thermal tolerances and depth preferences to predict changes  
258 in distribution of marine species. Applying this approach for >13,000 marine species, García  
259 Molinos *et al.* [33] found that biodiversity would decrease in equatorial regions, but increase  
260 in others, and there would be a spatial homogenization of biodiversity by 2100. Recent  
261 observations of marine communities confirm those results in response to climate change  
262 [51, 52]. However, the likelihood of a response, and a subsequent shift in range mirroring  
263 climate velocity, is species-specific. For example, opportunities for the expansion and risk  
264 of contraction of a geographical range will depend on changes in the local climate space  
265 relative to a species' physiological tolerances (see Box 1, Figure II). Even if a geographical  
266 shift is triggered by changes in climate, different dispersal capacities of species result in  
267 range shifts that keep pace with, lag or even exceed rates of climate displacement [53-60].  
268 Range shifts will also depend on the interaction between climate change and external  
269 directional forces. In a recent global meta-analysis [61], statistical models combining the  
270 effect of climate velocity and its alignment with ocean currents explained a significantly  
271 higher proportion of the variance in observed range shifts for marine species globally than  
272 models based only on climate.

273

## 274 **Enhancing use of climate velocity in conservation**

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

280

### 281 *1. Tailoring climate velocity to be more biologically meaningful*

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

302 than a single, unidirectional source-to-destination pathway [66]. This reflects a more realistic  
303 scenario, where the location of the future climate analogue and the optimal route to reach it  
304 are unknown *a priori*.

305

306 Changes in climate can also manifest differently depending on season, and this seasonal  
307 signal can be obscured in annual means that are usually used in calculating climate velocity.  
308 Tailoring climate velocity to match temporal windows of biological processes or life stages  
309 could therefore provide more meaningful information for conservation (see example in  
310 Figure S3). For example, maximum and/or minimum monthly temperature or precipitation  
311 [26, 32, 34, 67] can be used to calculate local or climate-analogue velocities when seasonal  
312 processes are under consideration [68]. Further, analysis of the seasonal local climate  
313 velocity could be complemented with the shift in the timing of fixed temperatures-to capture  
314 the onset or termination of seasonal processes [18]. The utility of combining metrics of  
315 climate velocity and timing has not yet been investigated.

316

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

327

328 It should be noted that in each instance, adding biological realism to climate velocity comes  
329 at a cost. The current lack of biological information in climate velocity in its simplest form

330 confers generality across a broad range of species. However, the more climate velocity is  
331 tailored to be more biologically meaningful, the more specific the metric becomes to the  
332 species under consideration. Thus, the path of increasing biological realism moves climate  
333 velocity towards species distribution models or other species-specific modelling approaches  
334 that potentially have better predictive ability, but require more species-specific information  
335 and are less generally applicable.

336

## 337 *2. Informing design of protected areas and their networks*

338 Protected areas need to be considered within a holistic ecosystem-based management  
339 approach that recognizes the interactive and cumulative impact of human activities [70].  
340 However, the consideration of climate change in the design and evaluation of protected  
341 areas is still in its infancy [71]. Here, climate velocity might be useful in several ways. First,  
342 climate velocity identifies regions where climate conditions are changing rapidly, or are  
343 projected to do so in the future. These regions might correspond to those where distribution  
344 shifts are more likely, particularly at range boundaries or for range-restricted species,  
345 potentially moving species out of the protected areas designed to protect them [72, 73].  
346 Further, current climate-velocity patterns can differ strongly from those projected for the  
347 future, highlighting the challenge of anticipating effects of a dynamic climate when designing  
348 static networks of protected areas (see Box 3). Second, climate velocity can be used to  
349 estimate climate residence time (Glossary) of different protected areas across a network  
350 (Box 3), indicating the required pace of adaptation to climate change. Areas of long climate  
351 residence times correspond to areas of low climate velocity. On land, however, areas of long  
352 residence times tend to be in mountainous terrain, perhaps contributing to the problem of  
353 residual reserves, that is, areas where conservation impact is low because the land is  
354 unsuitable for conversion or extraction of natural resources [74, 75]. Third, climate velocity  
355 can also be interpreted in terms of the opportunities for range expansions via dispersal and  
356 colonization from local populations at the leading edge of a species' distribution. Here,  
357 establishing the connectivity between current and future climates will be important for

358 anticipating whether the existing network of protected areas will capture those expansions.  
359 For example, climate-velocity trajectories [24] used for this purpose can reveal emergent  
360 classes of isotherm shifts [76], which could be relevant to biology and ultimately used to  
361 inform conservation actions (Box 3).

362

### 363 *3. Conserving ocean biodiversity in three dimensions*

364 In the ocean, climate velocity has mainly been applied to surface temperatures (e.g., [33,  
365 50, 77]), which are probably relevant for epipelagic (0-200 m) marine groups, including all  
366 photosynthetic organisms that need to remain within the sunlit zone (the top 200 m). But in  
367 the open ocean, mesopelagic (200-1000 m) and bathypelagic (1000-4000 m) marine groups  
368 live below this sunlit zone, and the magnitude and direction of climate velocity might change  
369 with depth, with important implications for conservation [78, 79] (Figure S4). For example,  
370 although there is less warming in the deep ocean relative to the surface [80], spatial  
371 gradients are likely to be gentler at depth, so it is unclear how the climate velocity might  
372 change with depth. Moreover, the direction of climate velocity could differ with depth,  
373 according to the spatial gradient of temperature in different ocean layers (Figure S4, also  
374 see the SOM of Hiddink *et al.* [21]), implying that species distributions might move in different  
375 directions with depth. Different horizontal speeds and directions of climate velocity with  
376 depth would influence whether organisms at different depths remain within a particular  
377 marine protected area with climate change [81], and whether communities at different  
378 depths and that interact, remain intact.

379

380 Not only can climate velocity be applied in horizontal slices in the ocean, but to the seafloor.  
381 Movements of organisms on the seafloor are restricted to a two-dimensional surface, as  
382 they are on land, and conventional two-dimensional climate velocity is therefore appropriate.  
383 As terrestrial species move to higher (cooler) elevations with warming, marine organisms  
384 on the seafloor have been observed to move to deeper (cooler) water with warming [20]  
385 (Figure S4). A pertinent conservation issue concerning seafloor communities is how best to

386 conserve seamounts, which have high levels of endemism and vertical habitat zonation [82],  
387 as mountains do on land. Applying local-climate velocity to seamounts could provide new  
388 insights into how these unique communities could respond to climate change. Seamounts  
389 also function as stepping stones for many animals across the abyssal plain [83], as  
390 mountains do on land. Applying climate-analogue velocity could provide new insights into  
391 how animals might move between seamounts in response to climate change, and help  
392 inform networks of protected areas for seamounts.

393

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

402

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

409

#### 410 *4. The potential of climate velocity to inform conservation actions*

411 Climate-velocity trajectories provide considerable scope to inform conservation actions (see  
412 Table S2 for trajectory classes [24, 76] and a summary of potential implications for species  
413 and conservation actions). For example, climate source areas (i.e., regions of novel climate



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

429

### 430 **Concluding remarks**

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

442

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453

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- 654

## 655 **Figures**

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

658

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

683 distances to reflect more realistically the influence of thermal gradients (climate connectivity)  
684 and other non-climate factors on the dispersal route between present and future analogues.  
685  
686 **Elements**  
687 Glossary  
688 BOX 1. The ecological context of climate velocity  
689 BOX 2. Caveats associated with climate velocity  
690 BOX 3. Methodological considerations when applying climate velocity  
691 BOX 4. A case study applying climate velocity, residence time and climate-velocity  
692 trajectories to the UK marine protected area network  
693 SI – Additional support figures and tables  
694



695 **Glossary**

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

705

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

713

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

717

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

720

721 **Local climate velocity:** The original climate-velocity metric [16] that has two main  
722 components in its calculation: a temporal trend and a spatial gradient, both for the same

723 climate variable (Fig. 1A). Local climate velocity is an estimate of the instantaneous climate  
724 velocity of an isoline at a location.

725 **Box 1. The ecological context of climate velocity**

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

737

738 Figure I. Understanding climate velocity on land.

739

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

750

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

753 (B) The distribution of a species showing separate populations (dark circles) across a  
754 latitudinal gradient at two times. Local population contractions and expansions are observed  
755 at each range edge at time  $t_2$ .

756

757 **Box 2. Caveats associated with climate velocity**

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

763

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

774

775 **Climate velocity currently has no standard measure of uncertainty.** There are many  
776 potential sources of uncertainty in estimates of climate velocity that are usually  
777 unacknowledged. These include (but are not limited to): (a) error in the gridded climate  
778 metrics that affect estimates of spatial gradient and temporal trend in the climate variable,  
779 and (b) variability both within individual climate projections (model runs) and among climate  
780 projections (different general circulation models and representative concentration  
781 pathways). Schliep *et al.* [90] go beyond the conventional finite-difference approach to  
782 climate velocity explained here by modelling temperature (as an example of a climate  
783 variable) as a function of both space and time within a stochastic Bayesian framework. This  
784 allows the quantification of variability associated with simultaneous estimates of spatial

785 gradients and temporal trends in temperature (i.e., uncertainty source (a) above). Although  
786 this process is numerically complex and computationally demanding, it is an important first  
787 step in quantifying uncertainty. Accounting for remaining sources of uncertainty require  
788 further research.

789

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

796

797 **Box 3. Methodological considerations when applying climate velocity**

798 *Which environmental variables?*

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

806

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

815

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

823

824 *What time scales?*

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

827

828 *What space scales?*

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

842

843 *Combining environmental variables?*

844 Climate velocity has usually been applied to an individual variable. When considering  
845 multiple variables (e.g., temperature and rainfall), these have generally been treated  
846 separately as independent drivers of species movement [17, 26, 32]. However, Hamann *et*  
847 *al.* [28] developed a multivariate approach to climate-analogue velocity based on a Principal  
848 Components Analysis of multiple metrics (e.g., minimum, maximum, mean) of temperature  
849 and rainfall. This approach has the benefit of considering the multivariate movement of  
850 climate space, but at the cost of complicating interpretation. Moreover, multivariate climate-  
851 analogue velocities are likely to be higher than corresponding univariate estimates [28, 34],  
852 since finding similar multivariate climates will often require a large search radius (i.e., similar



853 rainfall is likely to be found closer than similar rainfall and temperature combined). The  
854 magnitude of this effect can be mitigated by relaxing assumptions defining analogue  
855 climates (e.g., expanding bandwidth to incorporate more climate variability [67]). Multivariate  
856 local climate velocity could be calculated by applying vector algebra to multiple univariate  
857 estimates of local climate velocity. For example, if there were two univariate climate  
858 velocities (e.g., temperature and rainfall) in opposing directions and equal in magnitude they  
859 would cancel. However, in general, the new multivariate climate space would not be the  
860 same as the original. This divergence in angles of such univariate estimates can be  
861 considered as a measure of climate stress on an organism and has provided insight into  
862 potential ecological responses to multivariate climate change [30].

863

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

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

881

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

889

890 Climate-velocity trajectories over the past 50 years are generally directed poleward along  
891 the English coast (Figure IE), suggesting that the coastal network currently exhibits good

892 connectivity (MPAs in the north should receive climate migrants from those in the south as  
893 temperature warms). However, climate-velocity trajectories until 2050, as projected from  
894 RCP8.5, show a different pattern on the east coast of the UK, where thermal niches move  
895 offshore into the North Sea towards Scandinavia (Figure IF). This scenario suggests that  
896 littoral species on this coast might be forced to adapt *in situ*, because they become  
897 disconnected from their current thermal niches. This could have management implications,  
898 especially for smaller protected areas on the east coast of Scotland, where residence times  
899 will continue to be short. Here, the possibility of assisted migration and translocations of  
900 species of concern might be considered.

901

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

908