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

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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

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-

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 is 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,

4

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., 95th 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

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

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

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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654

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

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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

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

723 climate variable (Fig. 1A). Local climate velocity is an estimate of the instantaneous climate

724 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.

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 *t2*.

756

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

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

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?

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

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

33

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.

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