Mapping climatic mechanisms likely to favour the emergence of novel communities

Alejandro Ordonez[1]*, John W. Williams[2,3] and Jens-Christian Svenning[1]

Climatic conditions are changing at different rates and in different directions[1,2], potentially causing the emergence of novel species assemblages[3]. Here we identify areas where recent (1901–2013) changes in temperature and precipitation are likely to be producing novel species assemblages through three distinct mechanisms: emergence of novel climatic combinations[4,5], rapid displacement of climatic isoclines[1,2,6–8] and local divergences between temperature and precipitation vectors[1,2]. Novel climates appear in the tropics, while displacement is faster at higher latitudes and divergence is high in the subtropics and mountainous regions. Globally, novel climate combinations so far are rare (3.4% of evaluated cells), mean displacement is 3.7 km decade^{-1} and divergence is high ($>60°$) for 67% of evaluated cells. Via at least one of the proposed mechanisms, novel species assemblages are likely to be forming in the North American Great Plains and temperate forests, Amazon, South American grasslands, Australia, boreal Asia and Africa. In these areas, temperature- and moisture-sensitive species may be affected by new climates emerging, differential biotic lags to rapidly changing climates or by being pulled in opposite directions along local spatial gradients. These results provide spatially explicit hypotheses about where and why novel communities are likely to emerge due to recent climate change.

Climate change is expected to cause individualistic range dynamics and the reshuffling of species into novel assemblages through at least three mechanisms. First, the opening up of currently unavailable portions of climate space, combined with differences among species in their preadaptation to novel climates[4,5,9]. Second, rapid rates of climate change and the differential dispersal ability of species to track rapid change[9–13]. Third, differences among climate variables in their spatial direction of change, combined with differences among species in their sensitivity to these climate variables[2,14]. Here, we refer to these three mechanisms as climate novelty, rate of displacement, and divergence. Using these concepts we provide spatially explicit hypotheses about where novel communities may emerge due to recent climate change and discuss their relative importance for community dynamics.

Multidimensional climatic changes produce individualistic organismal responses, from which novel communities can emerge. For example, the responses to historical climate change (1950–2010) by 464 Australian bird species[14] were underestimated when considering only temperature. Some Californian plant species have shifted downhill during the twentieth century despite the expected upward shift due to rising temperatures, a pattern possibly associated with changes in water balance[15] (however, see ref. 16). Similarly,

individualistic range dynamics are a hallmark of species distributions during past glacial–interglacial cycles[17], with the opening up of 'no-analogue' climates linked to shifts in species-realized climatic niches[9] and the formation of novel species assemblages[5,18,19]. Interspecific differences in dispersal ability and response time to climate change are well established and will produce communities shaped by both equilibrial and disequilibrial processes[5,13].

Here, we focus on assessing where climate change for the 1901–2013 period is most likely to promote the formation of novel species assemblages via climate novelty (dissimilarity in climatic combinations between early twenty-first-century climate and early twentieth-century conditions; Fig. 1a), displacement (average speed of climate velocity vectors for the 1901–2013 period; Fig. 1b), and divergence (angle between climate velocity vectors for the 1901–2013 period; Fig. 1c). We focus on the possible impacts of recent climatic changes to develop spatially explicit hypotheses of how novel communities might emerge that are model- and scenario-independent. To our knowledge, no attempt has been made to evaluate these three mechanisms simultaneously or combine them into a single assessment of drivers of community novelty at the scale (global) and resolution (2.5 arcmin) achieved here.

Using the minimum standardized Euclidean distance (SED$_{min}$ and Methods), we determined the novelty of early twenty-first-century climates relative to early twentieth-century climates, as in ref. 20. We then determined both the speed and bearing of temperature and precipitation velocity vectors. The speed of climate velocity vectors represents the rate of climate isocline movement. The vector bearing describes the direction of movement. Displacement was calculated as the mean speed of individual temperature and precipitation velocity vectors, without reference to direction (Fig. 1b and Supplementary Fig. 1). Divergence was calculated as the angle between temperature and precipitation velocity vectors (Fig. 1c), so it indicates whether species tracking temperature and precipitation changes will be pulled in similar or different directions (Supplementary Fig. 1). Low divergence (values close to 0°) means that temperature and precipitation changes should pull climate-sensitive species in the same direction, either because temporal and precipitation changes are temporally concordant (for example, warming and wetting) in a region with concordant spatial gradients, or because temporal and precipitation changes are locally opposite (for example, warming and drying) in a region with locally opposite climatic gradients. High divergence (values from 90° to 180°) means that climate changes should pull climate-sensitive species in orthogonal or opposite directions relative to the local spatial gradients, depending on the species' sensitivity to temperature and moisture changes.

[1]Section of Ecoinformatics and Biodiversity, Department of Bioscience, Aarhus University, Ny Munkegade 114, DK-8000 Aarhus C, Denmark. [2]Center for Climatic Research (CCR), University of Wisconsin, Madison, Wisconsin 53706, USA. [3]Department of Geography, University of Wisconsin, Madison, Wisconsin 53706, USA. *e-mail: alejandro.ordonez@bios.au.dk
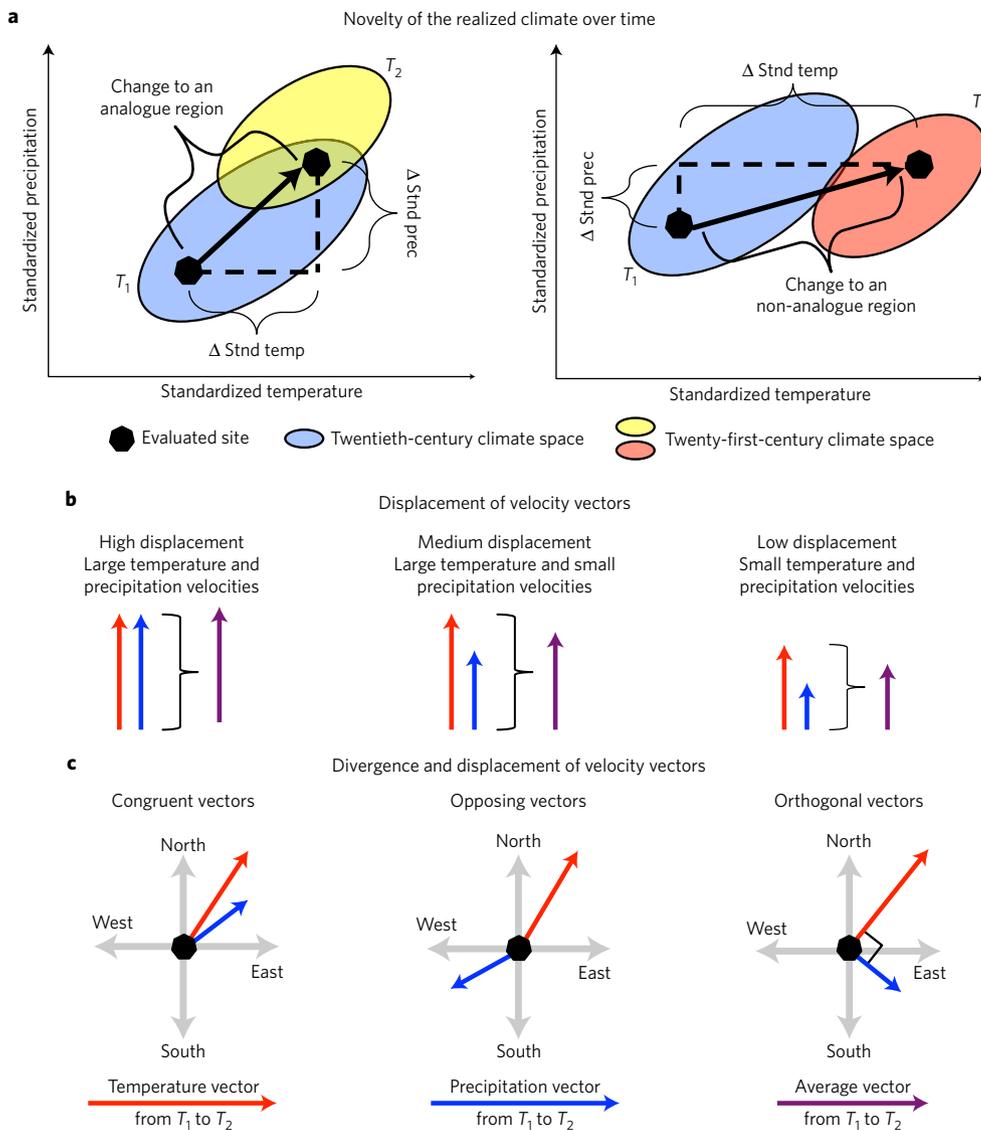
Figure 1 | Diagram representing the differences between climatic novelty, displacement and divergence. Climatic novelty, displacement and divergence can produce non-analogue species assemblages. **a**, Novelty measures whether the climates for a particular location within a region (blue ellipse) will move into previously realized (left panel) or unrealized (right panel) portions of climate space using the SED (defined by $\sqrt{(\Delta \text{Stnd prec})^2 + (\Delta \text{Stnd temp})^2}$, where Stnd prec is standardized precipitation and Stnd temp is standardized temperature) in climatic conditions between past (T_1) and present (T_2) realizations as described in ref. 5. **b,c**, Displacement (**b**) and divergence (**c**) are primarily local measurements that are assessed in geographic space as the average rate of movement of climatic isoclines (red, blue and purple vectors), and the differences in direction among climate velocity vectors, which integrate both the local spatial gradients and the direction of temporal changes.

Novelty, displacement, and divergence are all partially interrelated, for example, novel climates can emerge via fast displacement and high divergence. However, novelty is primarily assessed in environmental space while displacement and divergence are primarily spatial phenomena. Specifically, novelty is a regional to global phenomenon, representing the emergence of climatic conditions unlike any in a reference baseline (Fig. 1a). By comparison, displacement (Fig. 1b) and divergence (Fig. 1c) assess local changes, and hence represent mechanisms for locally reshuffling species into new combinations by populations tracking climate change at different rates and directions.

The speeds of the temperature and precipitation vectors were weakly correlated (Dutilleul's corrected Pearson's $\rho = 0.03$; $p < 0.001$; $n = 9{,}120{,}848$), with a 0.72 km decade^{-1} mean difference (Fig. 2) and wide variability across biomes (Supplementary Table 1). Unsurprisingly, these estimates were slower than previous historical estimates based on 1°-resolution climate surfaces[7], and were

comparable to near-future estimates based on 1-km-resolution climate surfaces[8], given the sensitivity of displacement estimates to data resolution (Supplementary Fig. 2 and ref. 1). These findings highlight the need to consider data resolution when making ecological interpretations of displacement rates.

The speed and distribution of SED$_{min}$ showed that novelty of 1993–2013 climates relative to 1901–1920 climates was rare and localized, but expected to increase over this century[4]. Only 3.5% of evaluated grid cells showed climates above the climate novelty threshold (SED$_t$ and Methods), and encompassed tropical regions, boreal forests, central Asia (Fig. 3a). Climatic novelty is expected to increase over this century[4]. The distribution of regions defined as novel was similar between multiple 20-year time periods, but novelty was larger for recent time slices (Supplementary Fig. 4).

Global mean displacement for the 1901–2013 period was 3.7 km decade^{-1}, with displacement estimates varying widely across biomes (Table 1). Displacement estimates varied with temporal
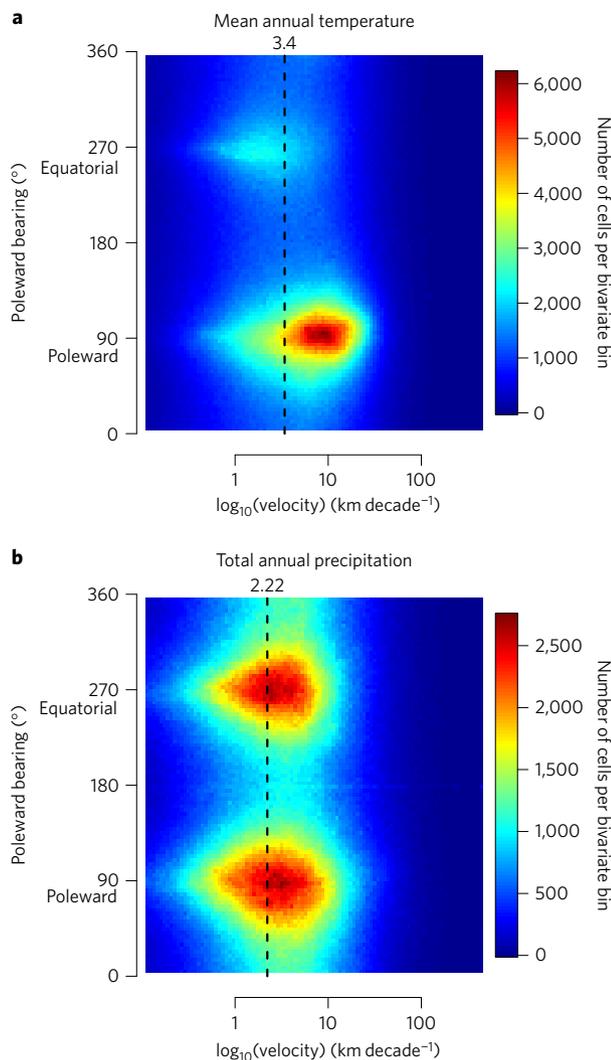
1105

a

b

Figure 2 | Bivariate kernel-density plots of the bearing and rate of displacement for temperature and precipitation from 1901 to 2013.
a,b, Kernel-density plots for temperature (in °C; **a**) and precipitation (in mm yr⁻¹; **b**) indicate the combined frequency (the number of cells per bivariate bin) of bearing (90° indicates a poleward direction and 270° indicates an equatorward direction of velocity vectors) and displacement (mean speed of change) across the globe. The dashed vertical line and value at top of each panel shows the geometric mean for global displacement.

grain, with century-scale displacement estimates lower than those measured for three 30-year intervals (Table 1). Displacement rates were fast across most parts of the globe (Fig. 3b), particularly in high-latitude regions with little topographic relief, such as boreal forests, and grasslands and savannahs in both temperate and flooded regions (Table 1).

Globally, the directionality of temperature vectors was strongly poleward, while precipitation directionality was more diverse and had strong poleward and equatorward components (Fig. 2). However, directionality varied widely among biomes (Supplementary Table 1). Divergences above 60° were common globally (grey to red colours; Fig. 3c), with a mean divergence of 100° (Table 1). Divergence was sensitive to data resolution, with lower divergence at coarser-scale analyses (Supplementary Fig. 3). Globally, divergence was orthogonal (60° to 120°) for 21% of evaluated cells, covering areas in the North American Great Plains, the Amazon Basin, Argentinean grasslands, northern Australia, eastern and central Africa, and the Indian subcontinent (grey; Fig. 3c),

indicating a disaggregation of temperature and moisture associations. Divergence was above 120° for over 43% of the cells, including Mediterranean Europe, temperate conifer forests and boreal forests across Russia, the Rocky Mountains, ice-free areas of East Greenland, and the southern coast of Australia (light red to red; Fig. 3c). In regions with temperature- and moisture-controlled ecotones, the prevalence of high divergence may cause ecotones and associated species to move in opposite directions. For example, in the Rockies, upper treeline appears to be influenced by temperature-related variables (for example, growing season length, winter severity) while lower treeline often is sensitive to moisture availability[15]. In areas of low divergence (∼33% of the evaluated cells), temperature and precipitation changes are less likely to pull species distributions and ecotones in different directions (Supplementary Fig. 1).

Displacement and divergence were weakly correlated (Dutilleul's corrected Pearson's $\rho = -0.042$; $p < 0.001$; Fig. 3e), highlighting the independence of these two vector-based metrics. Mapping displacement and divergence angles together (Fig. 3d) highlighted areas where the observed movement of climatic isoclines could produce regionally novel species assemblages in the near future. For the most part, areas with high displacement and divergence differ from those areas expected to experience the emergence of globally novel climates (Fig. 3a). The variable governing the bivariate spatial pattern was divergence (Fig. 3d). The most typical combination of divergence and displacement values were 0.25 to 10 km decade⁻¹ and 150° to 180° (Fig. 3e). We found areas with fast displacement and orthogonal to opposing divergences in all continents and regions (red colours; Fig. 3d). In such situations, the likelihood of species assemblage disaggregation may be relatively high. Slow displacement and low divergence combinations (light blue colours, Fig. 3d) were prevalent in areas with extensive topographic variability (the Rockies, Andes, Himalayas, and the Alps), continental China, Madagascar and central and northern regions of Africa. In such situations, the likelihood of community disaggregation is relatively low.

Our analyses provide spatially explicit testable hypotheses for where novel species assemblages could be emerging as a result of climatic novelty and the displacement and divergence of climatic isoclines over the past century. First, novel climates have emerged over the past 20 years in tropical and polar areas when compared to 1901–1920. Ongoing climate change might lead to the formation of novel species associations as climatic novelty continues to increase[4,5], as has occurred in the past[18,19]. Second, spatial rates of movement of climatic isoclines and for individual and combined climatic variables are as fast, and in many cases faster than the reported dispersal capacity for a wide array of organisms. Our displacement estimates of ∼3.7 km decade⁻¹ for the past century (1901–2013) are either similar to, or slower than, mean estimates of range changes for birds, butterflies and alpine herbs during the late twentieth century (∼6.1 km decade⁻¹; ref. 10). Similarly, displacement estimates of ∼11.1 km decade⁻¹ for the 1975–2013 period are slower than mean range changes of multiple groups of flying insects, birds, fishes and mammals during the early twenty-first century (16.9 km decade⁻¹; ref. 11), but faster than the IPCC Fifth Assessment Report estimates of species migration rates[21]. As species differentially respond to climate changes, a mismatch between climate shifts and species responses could result in the reduction, extirpation, or extinction of species with limited dispersal ability or small distributions, and the formation of disequilibrium communities[13]. The apparent mismatch between climate displacement and species dispersal capacity might be reduced as velocity estimates are evaluated using spatial resolutions that more closely represent the scale at which organisms experience their environment. However, as the rate and speed of climate change increases, the buffering effect of small-scale heterogeneity should be reduced.
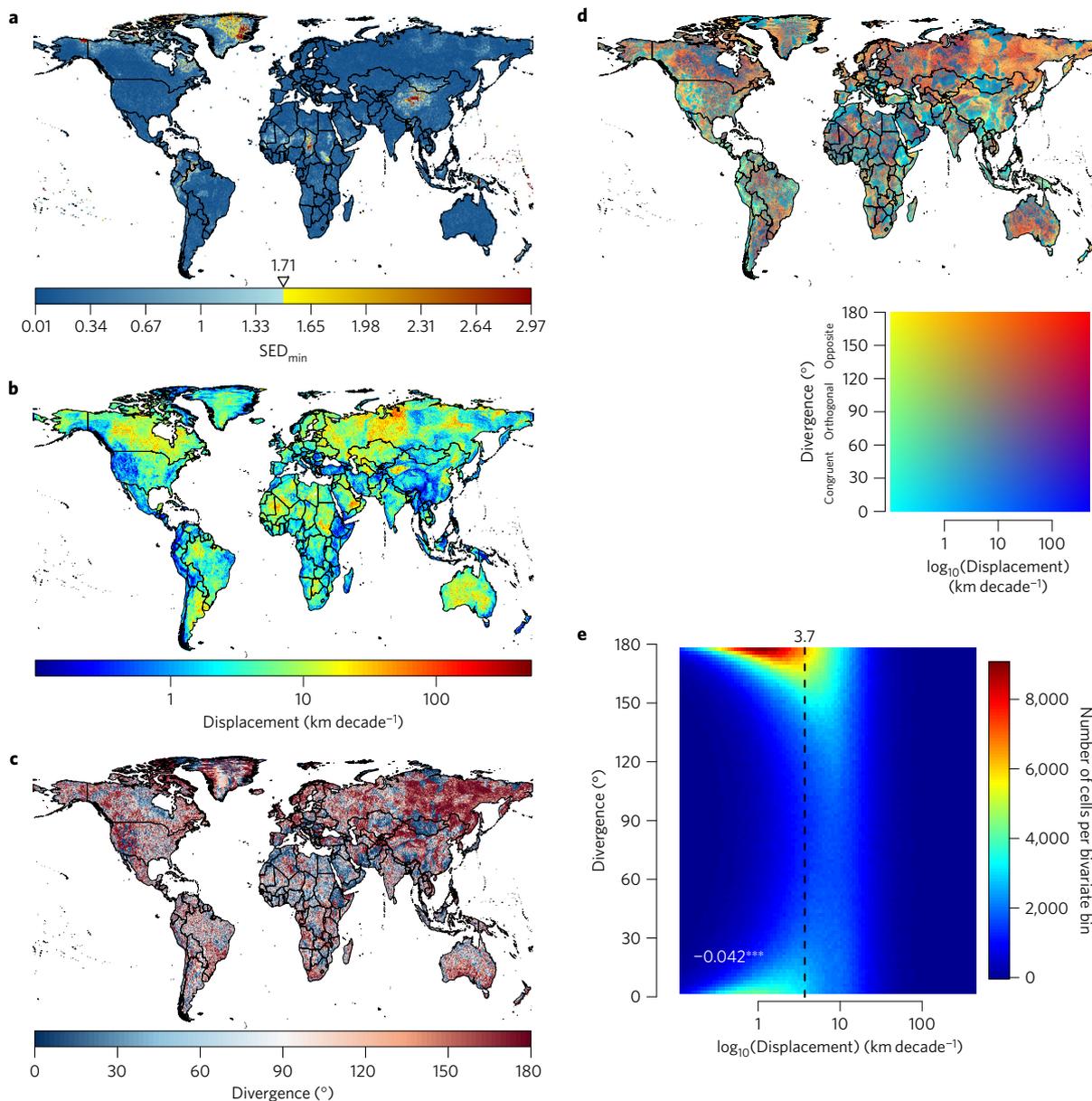
Figure 3 | Global maps of climatic novelty, average displacement, divergence, and combined divergence and displacement, with kernel-density plots of divergence and displacement for the period 1901–2013. a, Climate novelty of 1993–2013 climates measured using the minimum standardized Euclidean distance (SED_{min}, unitless) to 1901–1920 climates. The threshold value here defining no-analogue climates (SED_t) is marked as a triangle in the colour bar; blue-to-cyan indicates $SED_{min} < SED_t$ and yellow-to-red indicates $SED_{min} > SED_t$. **b**, Displacement is measured as average speed of climate velocity vectors. **c**, Divergence is measured as the angle between temperature and precipitation vectors, which determines the direction of movement required to track shifting climatic conditions by integrating both the local spatial gradient and the direction of temporal changes (Supplementary Fig. 1). **d**, Bivariate maps represent the combined realization of divergence and displacement values, where the associated colour legend shows the colour of all possible divergence and dispersal combinations. **e**, Kernel-density plots indicate the combined frequency (number of cells per bivariate bin) of displacement and divergence values across the globe, with the black dashed line and value representing the mean global displacement. The value in white shows the correlation between displacement and divergence. ***$P < 0.001$.

Third, the high divergence in many regions might result in many species not following the range shifts expected from temperature-only assessments[10,11]. Species may increasingly face a situation where tracking the optimal environmental requirements is no longer possible, as the direction of movement of temperature and hydrological conditions go in opposite directions, and may be disrupting the underlying climatic gradients. Climate divergence might explain the downward altitudinal range shifts of some tree species in North America[15] and Europe[22] despite rising temperatures (but see ref. 16). Similarly, the individualistic response of plants and other species to climatic changes accompanying the last

deglaciation[9] has been shown to result in a rearrangement of species assemblages[18].

As the effects of climate change are likely to intensify, being able to identify how and where these changes can generate new species assemblages has important implications for conservation. For example, where displacement is fast, conservation strategies could include managed relocation of dispersal-limited species, while conservation priorities could focus on protecting desired microclimatic combinations in slow-displacement areas with large divergences. In areas with intermediate environmental disturbance, facilitating ecosystem adaptation[23] and preserving the geophysical

Table 1 | Summary of the geometric means of the average displacement distance and means for the divergence angles.

Biomes	Vector displacements (km decade^{-1})				Vector divergence (°)			
	1901–2013	1901–1945	1945–1975	1975–2013	1901–2013	1901–1945	1945–1975	1975–2013
Boreal forests/taiga	7.19	11.60	12.40	17.00	122.2	108.6	89.0	113.0
Deserts and xeric shrublands	4.58	6.89	11.16	15.68	89.0	83.5	91.5	80.5
Flooded grasslands and savannahs	8.37	11.17	13.41	27.84	102.5	83.7	87.0	85.1
Mangroves	4.30	6.90	11.49	16.97	94.1	86.0	86.0	97.3
Mediterranean forests, woodlands and scrub	2.13	3.97	6.33	5.14	79.7	87.0	85.6	92.9
Montane grasslands and shrublands	1.20	1.88	3.25	4.61	95.3	84.4	84.7	92.4
Temperate broadleaf and mixed forests	3.47	5.40	8.44	10.72	105.8	90.4	85.0	100.2
Temperate conifer forests	1.36	2.99	3.56	3.62	104.0	90.5	81.7	90.0
Temperate grasslands, savannahs and shrublands	5.38	9.07	9.86	11.85	100.4	87.6	88.7	93.8
Tropical and subtropical coniferous forests	0.87	1.44	2.33	2.55	101.6	87.5	74.5	82.3
Tropical and subtropical dry broadleaf forests	2.03	3.47	5.79	6.91	98.0	85.7	89.8	92.9
Tropical and subtropical grasslands, savannahs and shrublands	3.52	7.01	11.01	11.14	86.7	92.6	85.4	93.7
Tropical and subtropical moist broadleaf forests	1.95	4.10	7.01	7.73	92.4	91.3	88.9	93.0
Tundra	3.85	5.75	9.70	13.86	111.1	93.4	79.6	98.6
Global mean	3.70	6.29	9.34	11.47	100.9	92.4	86.4	94.9

Displacement is measured as the average magnitude of the climate velocity vectors, and divergence as the angle between the temperature and precipitation vectors, bounded between 0° and 180° (see Methods).

diversity[24] could be the best strategy. Areas with high global novelty are particularly exposed to ecological surprises[19] and have a critical need for long-term adaptive management experiments[20]. These recommendations are not intended to provide specific guidance to managers, but rather highlight how these mechanisms may cause management responses to have differing relevancy in the different areas.

The relative importance of climate novelty, displacement, and divergence as mechanisms for community reshuffling assembly remains an open question. The spatial patterns of novelty, displacement, and divergence differ strongly from each other, and hence make different predictions about where novel communities are likely to arise. Importantly, many species distributions are lagging climate change[13], so that the emergence of novel communities in response to the past century's climate changes may still be under way. Climate is just one of many changing factors, and species distributions are, and will be, determined by a broad array of factors in addition to climate[25]. The interaction of factors such as land use and anthropogenic species introductions with climate may strongly shape species range dynamics in response to climate change and are likely to affect how biodiversity dynamics in response to climatic novelty, displacement, and divergence will play out.

Methods

Methods and any associated references are available in the [online version of the paper](#).

References

1. Dobrowski, S. Z. *et al*. The climate velocity of the contiguous United States during the 20th century. *Glob. Change Biol.* **19,** 241–251 (2013).
2. Ordonez, A. & Williams, J. Projected climate reshuffling based on multivariate climate-availability, climate-analog, and climate-velocity analyses: implications for community disaggregation. *Climatic Change* **119,** 659–675 (2013).
3. Hobbs, R. J., Higgs, E. S. & Hall, C. *Novel Ecosystems: Intervening in The New Ecological World Order* (John Wiley, 2013).
4. Williams, J. W., Jackson, S. T. & Kutzbach, J. E. Projected distributions of novel and disappearing climates by 2100 AD . *Proc. Natl Acad. Sci. USA* **104,** 5738–5742 (2007).
5. Jackson, S. T. & Overpeck, J. T. Responses of plant populations and communities to environmental changes of the late Quaternary. *Paleobiology* **26,** 194–220 (2000).
6. Ordonez, A., Martinuzzi, S., Radeloff, V. C. & Williams, J. W. Combined speeds of climate and land-use change of the conterminous US until 2050. *Nat. Clim. Change* **4,** 811–816 (2014).
7. Burrows, M. T. *et al*. The pace of shifting climate in marine and terrestrial ecosystems. *Science* **334,** 652–655 (2011).
8. Loarie, S. R. *et al*. The velocity of climate change. *Nature* **462,** 1052–1055 (2009).
9. Ordonez, A. Realized climatic niche of North American plant taxa lagged behind climate during the end of the Pleistocene. *Am. J. Bot.* **100,** 1255–1265 (2013).
10. Parmesan, C. & Yohe, G. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421,** 37–42 (2003).
11. Chen, I. C., Hill, J. K., Ohlemüller, R., Roy, D. B. & Thomas, C. D. Rapid range shifts of species associated with high levels of climate warming. *Science* **333,** 1024–1026 (2011).
12. Ordonez, A. & Williams, J. W. Climatic and biotic velocities for woody taxa distributions over the last 16 000 years in eastern North America. *Ecol. Lett.* **16,** 773–781 (2013).
13. Svenning, J.-C. & Sandel, B. Disequilibrium vegetation dynamics under future climate change. *Am. J. Bot.* **100,** 1266–1286 (2013).
14. VanDerWal, J. *et al*. Focus on poleward shifts in species' distribution underestimates the fingerprint of climate change. *Nat. Clim. Change* **3,** 239–243 (2012).
15. Crimmins, S. M., Dobrowski, S. Z., Greenberg, J. A., Abatzoglou, J. T. & Mynsberge, A. R. Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. *Science* **331,** 324–327 (2011).
16. Hijmans, R. J. Comment on "Changes in climatic water balance drive downhill shifts in plant species' optimum elevations". *Science* **334,** 177 (2011).
17. Davis, M. B. Pleistocene biogeography of temperate deciduous forests. *Geosci. Man* **13,** 13–26 (1976).
18. Williams, J. W., Shuman, B. N., Webb, T., Bartlein, P. J. & Leduc, P. L. Late-Quaternary vegetation dynamics in North America: scaling from taxa to biomes. *Ecol. Monogr.* **74,** 309–334 (2004).
19. Williams, J. W. & Jackson, S. T. Novel climates, no-analog communities, and ecological surprises. *Front. Ecol. Environ.* **5,** 475–482 (2007).
20. Radeloff, V. C. *et al*. The rise of novelty in ecosystems. *Ecol. Appl.* **25,** 2051–2068 (2015).
21. Field, C. B. *et al*. In *Climate Change 2014: Impacts, Adaptation, and Vulnerability* (eds Field, C. B. *et al*.) 35–94 (IPCC, Cambridge Univ. Press, 2014).
22. Lenoir, J., Gegout, J. C., Marquet, P. A., de Ruffray, P. & Brisse, H. A significant upward shift in plant species optimum elevation during the 20th century. *Science* **320,** 1768–1771 (2008).

23. Millar, C. I., Stephenson, N. L. & Stephens, S. L. Climate change and forests of the future: Managing in the face of uncertainty. *Ecol. Appl.* **17,** 2145–2151 (2007).
24. Anderson, M. G. & Ferree, C. E. Conserving the stage: climate change and the geophysical underpinnings of species diversity. *PLoS ONE* **5,** e11554 (2010).
25. Parmesan, C. *et al*. Beyond climate change attribution in conservation and ecological research. *Ecol. Lett.* **16,** 58–71 (2013).

Acknowledgements

Author contributions

A.O. developed and implemented the methodological approaches, downscaled the climatic data, ran analyses and produced figures and tables. A.O., J.W.W. and J.-C.S. interpreted the results. A.O. led the writing, with the assistance of J.W.W. and J.-C.S.

Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to A.O.

Competing financial interests

The authors declare no competing financial interests.

Methods

Monthly climate data for the 1901–2013 period came from the Climate Research Unit (CRU)[26]. Monthly values for each year were statistically downscaled to a resolution of 2.5 arcmin, using a change-factor approach[27]. Specifically, the anomaly in monthly climatic conditions between a target year and a baseline period (1950–2000) were bilinearly interpolated from their original 30 arcmin resolution to the desired resolution and then added to a 2.5 arcmin resolution baseline debased data set[28] for the 1950–2000 period. Annual temperature and precipitation for each year between 1991 and 2013 were estimated using downscaled monthly values. We focus on historic climate changes to have a model- and scenario-independent assessment of climatic change. We focus on temperature and precipitation for simplicity, and because they correlate to various relevant variables defining broad-scale limits to species distributions, organismal performance, and the rate of ecosystem processes.

This study is centred on the idea that environmental, ecological, and functional novelty arises via three complementary mechanisms. Opening up of currently unavailable portions of climate space, combined with differences among species in preadaptation to these novel climates[4,5,9]; rapid rates of climate change and the differential dispersal ability of species to track fast changes[9–13]; differences in climate variables in their spatial direction of change when compared to the local spatial gradient, combined with differences among species in their sensitivity to these climate variables[1,2,14]. We refer to these three distinct drivers of species reshuffling as climate novelty, rate of displacement, and divergence.

The speed and direction of velocity estimates depend on the spatial resolution and temporal domain of the climate input data[1]. Hence, we evaluated the sensitivity of displacement and divergence estimates to these two factors (Supplementary Fig. 3), using climate data at three additional resolutions (5′, 10′ and 30′) and for three periods of historical climate in the recent past (1901–1945, 1945–1975 and 1976–2000). CRU yearly estimates were downscaled to each of the evaluated resolution domains using a change-factor approach[27].

Estimating climatic novelty. We start by evaluating climatic dissimilarity between each cell under early twenty-first-century (1993–2013) conditions and to all land cells on Earth describing early twentieth-century (1901–1920) conditions using the standardized Euclidean distance (SED)[2,4]: $\mathrm{SED}_{i,j} = \sqrt{\sum_{k=1}^{2}((b_{k,i} - a_{k,j})^2/S_{k,j}^2)}$, where $a_{k,i}$ and $b_{k,j}$ are early twentieth-century and early twenty-first-century means for temperature and precipitation at grid cell i and j respectively, and $S_{k,j}^2$ is the interannual variability for early twentieth-century conditions. We also measured climatic dissimilarity to early twentieth-century conditions for four other 20-year periods: 1920–1940, 1941–1960, 1961–1980 and 1981–2000. Climate conditions were summarized as 20-year means to reduce the effect of interannual and decadal variability and extreme events. Climate novelty of the evaluated 20-year periods was assessed using the minimum SED (SED_{min}) for each grid cell (higher SED_{min} indicates high climate novelty). Given the extent of our study, comparability with previous studies[2,4] and to have a standardized global assessment of novelty, the mean of the 95th percentile of SED_{min} across all biomes was used to determine an SED threshold (SED_t) that determines when an SED value is large enough to represent a genuinely novel climate.

Estimating displacement and divergence. Both displacement and divergence are multivariate indices that are calculated from univariate indices of climate velocity[8]. Vector speed and directionality were determined using globally projected climatic rasters (using a equidistant cylindrical projection), to avoid latitudinal biases in the speed of vectors. Climate velocity combines the spatial gradient of climate conditions and the temporal trajectory of climate change for a location[1], providing a spatially explicit standardized measure of the expected movement rate and direction need to track the current conditions of a climatic variable[8]. Following the formulation in ref. 1, velocity vectors were estimated for the period 1901–2013 as: $V_I = ((d_c/d_t)/(d_c/d_x), (d_c/d_t)/(d_c/d_y))$, where d_c/d_t represents the change in a climate variable per unit time (temporal trends), and $d_c/d_{x,y}$ is the change in the same variable per unit of distance (local spatial gradient). For each grid cell, temporal trends were measured as the slope of generalized least squares linear regression, using an autoregressive term to account for temporal autocorrelation. Following the approach in ref. 7, local spatial gradients and bearings were calculated using a 3 × 3 neighbourhood (to maximize the effective spatial resolution of the analysis[8]). For this, we used the vector sum of the latitudinal and longitudinal gradient, while the associated vector bearing was used to determine the direction of the historical local spatial gradient. Following ref. 29, we use the convention that gradient vectors point from high to low values (Supplementary Fig. 1). For the estimation of the spatial gradient and bearing, we start by identifying the 3 × 3 neighbourhood cells. For each cell, the latitudinal gradient was calculated as the mean of the differences between each northern and southern immediate pair within the 3 × 3 neighbourhood. The longitudinal gradient was calculated as the mean of the differences between each western and eastern immediate pair within the 3 × 3 neighbourhood. Under this scheme, positive values indicate a northward or eastward directionality, while negative values

indicate the opposite. The direction of the pre-existing temperature and precipitation spatial gradients was defined as the angle between the latitudinal and longitudinal components, and the speed of the resulting vectors indicates the magnitude of the local spatial gradient (Supplementary Fig. 1).

The pre-existing spatial gradients exert a strong influence on the bearing and speed of climate velocities determining the temporal gradients. Climate velocities are determined by both the magnitude and direction of projected temporal changes and the underlying latitudinal and topographic effects on climatic gradients. As such, climate velocity vectors are always parallel to the direction of the pre-existing gradient, going in the same direction when the variable is increasing (from high to low values), or in the opposite direction when a variable is decreasing (from low to high values). The overall match in the magnitude of spatial patterns and bearings of climate velocity vectors to those presented in ref. 7 that are based on 60 arcmin maps indicate a consistency of climate velocity estimates to alternative data sources.

We define rate of displacement as the rate at which a species would need to move to keep pace with changing environmental conditions. Therefore, displacement was measured as the mean speed of temperature and precipitation velocity vectors, and so represents the average rate at which climate isoclines move (Supplementary Fig. 1). Our displacement metric is related to the way species and population distributions would have to shift to remain within a similar climatic range. This may be particularly important at distribution edges, as interspecific differences in dispersal capacity[30] between the leading and trailing distribution edges may lead to disequilibrial communities[12,13] in areas of high rates of climatic displacement.

Divergence was calculated as the angle between temperature and precipitation vectors, which determines the direction of movement required to track shifting climatic conditions based on the spatial gradient of the environmental variable and the direction of the temporal changes (Supplementary Fig. 1). It compares the direction of movement of individual climate variables, and is intended to assess whether temporal temperature and precipitation changes will pull species in the same or opposite directions relative to the local spatial gradient. To measure divergence we defined the following two terms and conventions:

The first is the spatial angle, which measures the angle between the local temperature and precipitation gradients. If the local spatial gradient trends from warm/wet to cool/dry, the spatial angle is defined to be 0°. Conversely, if a spatial gradient trends from warm/dry to cool/wet, the spatial angle is 180°. The rationale for setting the spatial angle to 0° is that temperature and precipitation variables are both trending from low to high values, hence are concordant, while 180° indicates that variables are trending in opposite directions. The spatial angle can be any value between 0° and 180° (Supplementary Fig. 1C).

The second is the temporal angle, which measures the directionality of temporal change in the precipitation and temperature variables. If both are increasing or both are decreasing, then the temporal response is 0°, versus an angle of 180° if one is increasing and the other decreasing (Supplementary Fig. 1F). Because time is one-dimensional, the temporal angle can only be 0° or 180°.

Our measurement of divergence is based on both the spatial gradient of the environmental variables (spatial angle) and the direction of the temporal changes (temporal angle). Divergence was then calculated as the absolute difference between the spatial angle and temporal angle (Supplementary Fig. 1H), which is equivalent to calculating divergence as the angles between the temperature and precipitation vectors. Hence, divergence here measures the discrepancy between the direction of local spatial gradient and the response to changing climatic conditions, ranging between 0° (low divergence) and 180° (high divergence). Conceptually, this approach is similar to the vector plots of spatial gradients and temporal trends introduced by ref. 29.

If we take a slightly simplified case in which temperature and precipitation gradients are either concordant or opposite to each other (Supplementary Fig. 1A,B), then there are four basic combinations of temporal changes and spatial gradients that can lead to either low or high divergence (Supplementary Fig. 1J):

The first combination is low divergence and low expected community shuffling because both temporal changes and spatial gradients are concordant: The local spatial gradients in temperature are concordant (that is, warm/wet to cold/dry) and the temporal changes are also concordant (warming and wetting). Under these conditions, the temporal changes pull species in the same direction as the local spatial gradient (Supplementary Fig. 1J, lower middle region).

The second combination is low divergence and low expected community shuffling because both temporal changes and spatial gradients are opposite. The local spatial gradients are opposite (that is, warm/dry to cold/wet) and temporal changes are also opposite (warming and drying). Under these conditions, the temporal changes push species in the same direction as the local spatial gradient (Supplementary Fig. 1J, upper middle region, where warming and drying is pushing species north).

The third combination is high divergence and high expected community reshuffling due to temporally opposite climate changes in regions with locally concordant spatial gradients (Divergence ∼ −180°). The local spatial gradients are

concordant (from warm/wet to cold/dry) but the temporal changes are opposite (warming and drying). Under these conditions the opposing temporal changes would be expected to pull temperature- and moisture-sensitive species in opposite directions along the locally concordant spatial gradient (Supplementary Fig. 1J, lowermost region). This situation is relatively uncommon (Fig. 3c, blue regions).

The final combination is high divergence and high expected community reshuffling due to temporally concordant climate changes in regions with locally opposite spatial gradients (Divergence ~180°). The local spatial gradients are opposite (from warm/dry to cold/wet) and the temporal changes are concordant (warming and wetting). Under these conditions the concordant temporal changes would be expected to pull temperature- and moisture-sensitive species in opposite directions along the locally opposite spatial gradient (Supplementary Fig. 1J, uppermost region).

In addition, many spatial gradients are orthogonal at local to regional scales. In these regions, changes in precipitation and temperature should be expected to pull moisture- and temperature-sensitive species in orthogonal directions. For example, in the Great Plains of central North America, rising temperatures over the past 100 years, combined with decreasing precipitation in a region characterized by a dry-to-wet west-to-east gradient, are expected to cause distributions of temperature-sensitive species to shift northwards, while moisture-sensitive species are likely to shift eastwards.

References

26. Harris, I., Jones, P. D., Osborn, T. J. & Lister, D. H. Updated high-resolution grids of monthly climatic observations—the CRU TS3.10 Dataset. *Int. J. Climatol.* **34,** 623–642 (2014).
27. Wilby, R. *et al*. *Guidelines for Use of Climate Scenarios Developed from Statistical Downscaling Methods* (IPCC, 2004); http://ipcc-ddc.cru.uea.ac.uk/guidelines/StatDown_Guide.pdf
28. Hijmans, R., Cameron, S., Parra, J., Jones, P. & Jarvis, A. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* **25,** 1965–1978 (2005).
29. Ackerly, D. D. *et al*. The geography of climate change: implications for conservation biogeography. *Diversity Distrib.* **16,** 476–487 (2010).
30. IPCC: Summary for Policymakers. In *Climate Change 2014: Impacts, Adaptation, and Vulnerability* (eds Field, C. B. *et al*.) 1–32 (Cambridge Univ. Press, 2014).