Projected distributions of novel and disappearing climates by 2100 AD

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Key risks associated with projected climate trends for the 21st century include the prospects of future climate states with no current analog and the disappearance of some extant climates. Because climate is a primary control on species distributions and ecosystem processes, novel 21st-century climates may promote formation of novel species associations and other ecological surprises, whereas the disappearance of some extant climates increases risk of extinction for species with narrow geographic or climatic distributions and disruption of existing communities. Here we analyze multimodel ensembles for the A2 and B1 emission scenarios produced for the fourth assessment report of the Intergovernmental Panel on Climate Change, with the goal of identifying regions projected to experience (*i*) high magnitudes of local climate change, (*ii*) development of novel 21st-century climates, and/or (*iii*) the disappearance of extant climates. Novel climates are projected to develop primarily in the tropics and subtropics, whereas disappearing climates are concentrated in tropical montane regions and the poleward portions of continents. Under the high-end A2 scenario, 12–39% and 10–48% of the Earth's terrestrial surface may respectively experience novel and disappearing climates by 2100 AD. Corresponding projections for the low-end B1 scenario are 4–20% and 4–20%. Dispersal limitations increase the risk that species will experience the loss of extant climates or the occurrence of novel climates. There is a close correspondence between regions with globally disappearing climates and previously identified biodiversity hotspots; for these regions, standard conservation solutions (e.g., assisted migration and networked reserves) may be insufficient to preserve biodiversity.

biodiversity hotspots | climate change | dispersal limitations | global-change ecology | ecological surprises

By the end of the 21st century, large portions of the Earth's surface may experience climates not found at present, and some 20th-century climates may disappear. The combination of high CO_2 concentrations, still-extensive ice sheets in Greenland and Antarctica, and current orbital and land–ocean configurations are geologically unprecedented (1). Already, CO_2 concentrations exceed any recorded for the last 650,000 years (2) and, without a substantive intervention, are projected to increase to 540–970 ppm (140–263% relative to 2000 levels) by 2100 AD (3). Global mean temperatures are projected to increase by 1.4–5.8°C by 2100 AD (3), with decreases in diurnal and seasonal temperature ranges (4) and spatially variable changes in precipitation. It is increasingly likely that some end-21st-century climates will include conditions not experienced at present ("novel" climates) and that some present climates may disappear. Here we statistically analyze 21st-century climate scenarios to map global risk surfaces for the occurrence of future novel and disappearing climates and discuss likely ecological impacts.

Climate is a primary constraint on species distributions and ecosystem function, and ecologists are faced with the challenge of forecasting species range shifts, extinction risks, biome shifts, altered disturbance regimes, biogeochemical cycling, and other ecological responses to climate change (5–7). Such forecasts are impeded by the difficulty of predicting ecological responses to environmental conditions outside the range of current experience. Niche theory predicts that multivariate changes in climate should cause shifts in species distributions, disruption of extant communities, and formation of novel species associations (8–10), because each species responds individualistically (Fig. 1). This conceptual framework is reinforced by observed ecological responses to the last deglaciation, which were characterized by large changes in species ranges, and, in places where past climates apparently lacked modern analogs, the development of species associations and biomes with no modern counterpart (11–13). Metaanalyses indicate already detectable responses to 20th-century temperature rises, with range shifts averaging 6.1 km per decade toward the poles (14, 15). Dispersal limitations may cause species responses to lag rapid climate change, promoting the formation of disequilibrial relationships between species distributions and climate. Others have argued that future novel climates may cause a reshuffling of communities (10, 12); however, our study attempts to move beyond generalities by explicitly mapping the future distribution of novel climates.

Conversely, species endemic to certain climates are at risk of extinction if those climates disappear, and communities in those regions may disaggregate or disappear (Fig. 1) (8). High-elevation and high-latitude species, for example, may go extinct as temperature or moisture changes drive vegetation zones upward and poleward (16–19). Rapid changes further enhance extinction risk by increasing the rate of climate change relative to the capacity of species to adjust by migration and colonization (8, 20).

Using model ensembles drawn from Intergovernmental Panel on Climate Change (IPCC) Assessment Report 4, we here calculate three indices of climatic risk: (*i*) local standardized climatic change, (*ii*) the climatic distance between the end-21st-century simulation for each gridpoint and its closest analog from the global pool of 20th-century climates (an index of the novelty of future climates), and (*iii*) the climatic distance between the 20th-century realization for each gridpoint and its closest 21st-century climatic analog (an index of the disappearance of extant climates). All three indices are based on the same metric of multivariate dissimilarity, and temporal differences are given context by comparing them against the multivariate differences in climate among modern potential biomes (see *Materials and Methods*). We use two nonmitigation emission scenarios, IPCC Special Report on Emissions Scenarios (SRES) A2 and B1, to span the range of IPCC emission scenarios (3). Finally, we

Fig. 1. Conceptual diagram showing the intersection among the fundamental niches for four species (Sp.; colored ellipses) and climatic envelopes for hypothetical 20th- and 21st-century climates (black-bordered ellipses) (8). Novel climates are the portions of the 21st-century envelope that do not overlap 20th-century climates, and disappearing climates are the portions of the 20th-century envelope that do not overlap 21st-century climates. Species cooccur only if their fundamental niches simultaneously intersect with each other and the current climatic space. Future climate change may cause a variety of ecological responses, including shifts in species distributions (species 1–3), community disaggregation (species 1 and 3), new communities forming (species 2 and 3), and extinction (species 4). This conceptual model assumes fixed niches, i.e., that climate change will outpace evolutionary adaptation (8).

analyze the effects of species dispersal limitations on these climatic risk indices.

Results

Local climate changes are large everywhere in the A2 scenario (Fig. 2A) but are largest in tropical and subtropical regions, with high values over most of Africa, South America, and southern Eurasia, as well as portions of eastern North America, the Arctic, and eastern Eurasia. In the A2 scenario, 56–100% of global land area is projected to experience biome-scale climate changes, versus 17–98% in the B1 scenario. This pattern (Fig. 2 A and B) differs from the fingerprint commonly associated with global warming [i.e., large increases in annual mean temperatures projected for circum-Arctic regions and northern hemisphere continental interiors (3)], because changes in all variables are standardized against their interannual variability (see *Materials and Methods*). Interannual temperature variability is smaller in low-latitude regions than in high-latitude regions, upweighting the statistical significance of tropical warming trends [2–4°C (A2) and 1–2.5°C (B1) mean annual warming by 2100 AD for the models used here]. Weighting by interannual variability also upweights the significance of temperature over precipitation changes because interannual variability for temperature is relatively small. Thus, the patterns shown in Fig. 2A and B primarily reflect standardized temperature changes.

The distribution of novel climates (Fig. 2 C and D) occupies a spatially cohesive subset of areas experiencing high local climate change. Novel climates are strongly concentrated in tropical and subtropical regions, with the highest dissimilarities over the Amazonian and Indonesian rainforests. Novel 21st-century climates are also projected for the western Sahara, low-lying portions of east Africa, eastern Arabian Peninsula, southeastern U.S., eastern India, southeast Asia, and northwestern Australia. The percentages of global land area with novel climates are 12–39% (A2) and 4–20% (B1). The clustering of novel climates in the tropics and subtropics and their scarcity in high latitudes suggest that a key determinant of the development of novel climates is the projected poleward shift of thermal zones. Tropical and subtropical areas also are projected to

experience large changes in precipitation, caused by an intensified hydrological cycle and shifted moisture advection (21), but these changes are secondary in the standardized indices used here. If the search for 20th-century analogs is limited to a 500-km radius, representing an upper limit to unassisted rates of plant migration by 2100 AD (see *Materials and Methods*), the extent of novel climates approximately doubles (Fig. 3 A and B) to 39–84% (A2) and 14–52% (B1).

Disappearing climates are primarily concentrated in tropical mountains and the poleward sides of continents (Fig. 2 E and F). Specific areas include the Columbian and Peruvian Andes, Central America, African Rift Mountains, the Zambian and Angolan Highlands, the Cape Province of South Africa, southeast Australia, portions of the Himalayas, the Indonesian and Philippine Archipelagos, and some circum-Arctic regions. There is generally little overlap between areas projected to develop novel climates and areas projected to have disappearing climates. The percentages of land area with disappearing climates are 10–48% (A2) and 4–20% (B1). Including a 500-km constraint increases the extent of disappearing climates to 37–85% (A2) and 14–50% (B1) (Fig. 3 C and D).

The risk of novel and disappearing climates scales linearly with the magnitude of mean global warming (Fig. 4), suggesting that there is no obvious threshold beyond which a "dangerous" level of climate change exists (22). However, ecological systems are likely to exhibit strongly nonlinear responses to climatic forcing (6), so that forecasting ecological responses to novel and disappearing climates will be critical.

Discussion

Different ecological risks are associated with the prospect of novel versus disappearing climates. Novel temperature regimes, combined with changes in precipitation, may lead to novel species associations and other unexpected ecological responses, as has occurred in the past (11–13). Because the pre-Industrial Revolution climate system was already in a warm state, further increases in temperatures are likely to be novel not just relative to the 20th century but also to climates for at least the last million years (20). Tropical species may be particularly sensitive to 21st-century warming because (*i*) tropical temperatures vary less than high-latitude temperatures at daily, seasonal, orbital, and tectonic timescales (23), and (*ii*) range size tends to decrease toward the equator (Rapoport's Rule) (24), so that tropical species are more narrowly endemic in both geographic and climatic space (25, 26). Ecosystem models suggest that Amazonia is at particular risk for increased fire frequency and loss of forest cover (7). The potential for ecological surprises in the tropics adds urgency to current conservation efforts.

Forecasting species-level responses to novel climates is a serious challenge, because they force an extrapolation of ecological niche models beyond the observed correlations among current species distributions and climates (8). Paleoecological data clearly indicate that some past plant communities and biomes had no modern analog (11–13) and likely grew in response to climates also lacking modern analogs (8, 11). Moreover, the lack of current analogs for future climates limits our ability to validate ecological model predictions. One partial solution is to use the past as a testing ground for ecological models (27). Although past climates also are not a good analog for future climates (1), paleoecological and paleoclimatic data can be used to evaluate the robustness of ecological models to environmental conditions outside the modern envelope.

Disappearing climates increase the likelihood of species extinctions and community disruption for species endemic to particular climatic regimes, with the largest impacts projected for poleward and tropical montane regions. Many have warned that climate change may drive certain species and ecosystems to extinction, e.g., in high latitudes (18), the South African Fynbos
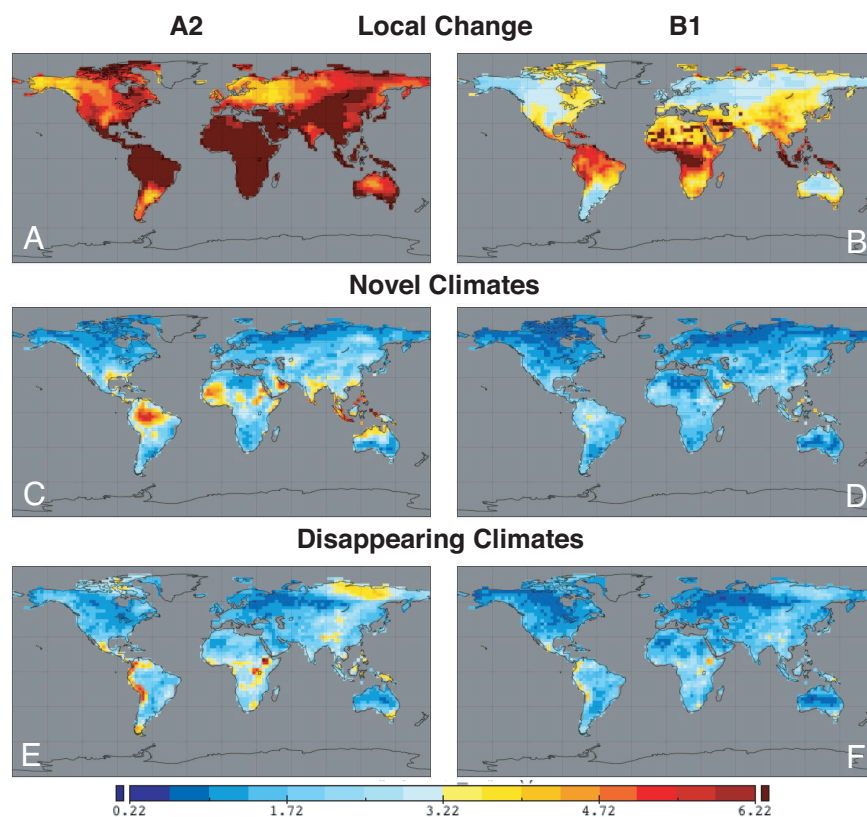
Fig. 2. Mapped indices of climate change risk for local climate change (*A* and *B*), novel 21st-century climates (*C* and *D*), and disappearing 20th-century climates (*E* and *F*). (*A*) Local climatic change for the A2 scenario, represented by the SED between the 20th- and 21st-century climate realizations for each grid-point. The color bar is scaled so that $SED \rightarrow SED_t$ (see *Materials and Methods*) are yellow to red. (*B*) As in *A* but for the B1 scenario. Locally high values over the Sahara, Arabian Peninsula, and southwestern Asia are an artifact of zero precipitation and precipitation variance simulated by the MRI–CGCM2.3.2 and CCSM3 models. In other models, the SED scores for these locations are similar to those of neighboring gridpoints. (*C*) Maps of the SED_{min} between the 21st-century realization for each gridpoint and the set of 20th-century climate realizations (A2 scenario). High dissimilarities indicate risk of novel climates. (*D*) As in *C* but for the B1 scenario. (*E*) Maps of the SED_{min} between the 20th-century realization for each gridpoint and the set of 21st-century climate realizations (A2 scenario). High dissimilarities indicate risk of disappearing climates. (*F*) As in *E* but for the B1 scenario. (*C–F*) The pool of potential climatic analogs is global.

(19), and neotropical cloud montane forests (16, 17). Our analysis places these regional alarms in a global context and goes further by showing that, in many cases, these climates may disappear entirely from the global set of end-21st-century climates. The areas of disappearing climates closely overlay regions identified as critical hotspots of biological diversity and endemism, including the Andes, Mesoamerica, southern and eastern

Africa, Himalayas, Philippines, and Wallacea (28). In these areas, elevated risks of extinction are likely, as is the disruption and disaggregation of extant communities (8).

Even with a conservative estimate of dispersal constraints, dispersal limitations greatly increase the risk that species will experience the loss of extant climates or the occurrence of novel climates (Figs. 2 and 3). Efforts to conserve biological diversity in the face
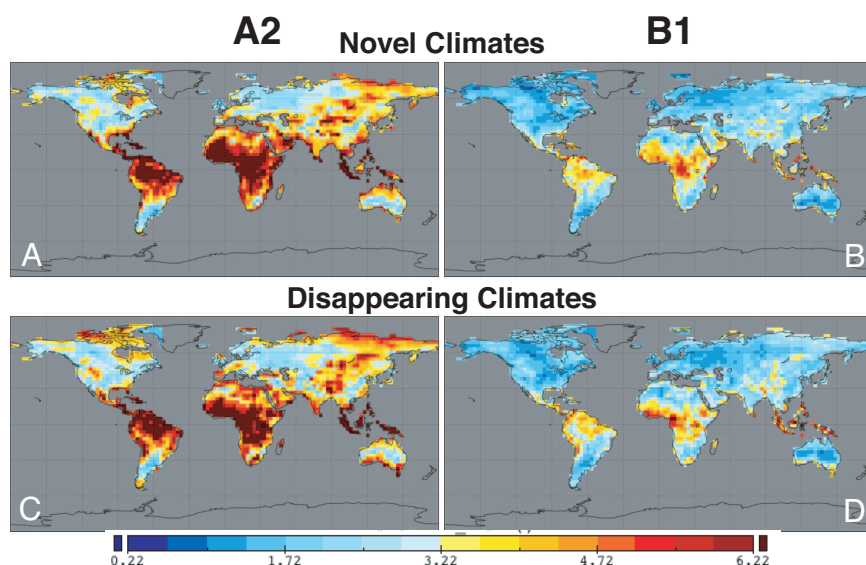
Fig. 3. *A–D* correspond to *C–F* in Fig. 1, except, here, the pool of potential analogs is restricted to gridpoints within 500 km of each target gridpoint. (*A*) SED_{min} between the 21st-century realization for each gridpoint and the set of 20th-century climate realizations (A2 scenario). High dissimilarities indicate risk of regionally novel 21st-century climates. (*B*) As in *A* but for the B1 scenario. (*C*) SED_{min} between the 20th-century realization for each gridpoint and the set of 21st-century climate realizations (A2 scenario). High dissimilarities indicate risk of regionally disappearing 20th-century climates. (*D*) As in *C* but for the B1 scenario.

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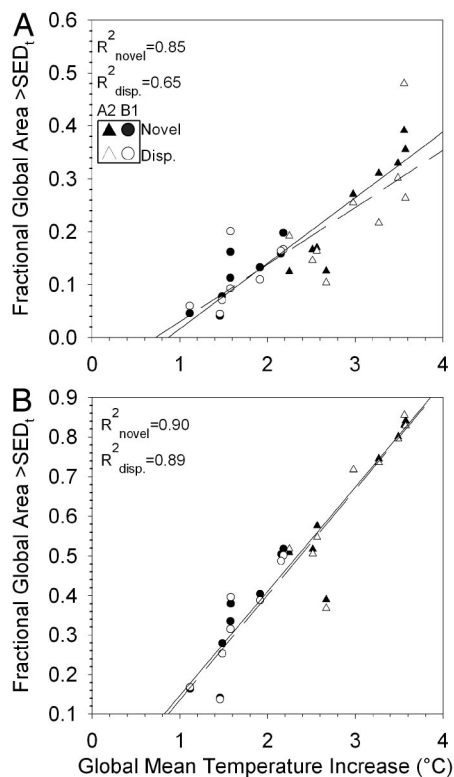
Fig. 4. Plots showing the relationship between global mean annual warming and the fractional global area with novel and disappearing climates. Each point represents an individual model; triangles represent A2 simulations, and circles represent B1 simulations. Filled symbols and the solid regression line represent risk indices for novel climates (corresponding to Figs. 2 *C* and *D* and 3 *A* and *B*); open circles and the dashed line represent risk indices for disappearing climates (corresponding to Figs. 2 *E* and *F* and 3 *C* and *D*). A2 and B1 scenarios are pooled for the regression model. (*A*) Search for climatic analogs is global (no dispersal constraint). (*B*) Search for analogs restricted to within 500 km (500-km dispersal constraint).

of climate change, e.g., by establishing dynamic networks of connected reserves that can facilitate species migrations (19) or "re-wilding" or otherwise assisting species migrations (29), may help overcome dispersal limitations. However, for those regions, communities, and species whose 20th-century climates lack 21st-century analogs anywhere globally (Fig. 2 *E* and *F*), such approaches will be insufficient. Furthermore, because of the spatial segregation between novel and disappearing climates (Fig. 2), species at risk of extinction due to disappearing climates are unlikely to be well positioned to take advantage of new climatic regimes.

No single analysis can capture all ecological risks associated with climate change, e.g., shifts in ecosystem distributions, changes in carbon sequestration, altered hydrological functioning, and increased fire frequency (e.g., refs. 7 and 30), so a variety is needed to capture the multidimensional responses of species and ecosystems to multidimensional climate change. Moreover, climate change is just one of many current ecological stressors. Interspecific differences in response time to the rapid pace of projected 21st-century climate change will also promote the formation of novel species assemblages and extinction risk (9). These factors, together with the projected development of novel climates and the threat that the climates particular to some biodiversity hotspots may disappear globally, create the strong likelihood that many future species associations and landscapes will lack modern analogs and that many current species and associations will be disrupted or disappear entirely.

Materials and Methods

We use a nine-model ensemble for the A2 scenario (856 ppm pCO$_2$ by 2100 AD) (3) and an eight-model ensemble for the B1 scenario (549 ppm pCO$_2$) [supporting information (SI) Table 1]. Each global climate model is represented by a single realization per scenario, chosen at random when multiple realizations were available. The equilibrium climate sensitivity of these models to CO$_2$ doubling is 2.1–4.4°C, with seven models between 2.7°C and 3.1°C (www-pcmdi.llnl.gov/ipcc/model_documentation/ipcc_model_documentation.php). All simulations were bilinearly interpolated to a common T42 grid ($\approx$2.8° × 2.8° resolution), the median resolution for the models used here.

After interpolation, we quantified dissimilarities between 20th- and 21st-century climates by using the standardized Euclidean distance (SED) (31):

$$\mathrm{SED}_{ij} = \sqrt{\sum_{k=1}^{4} \frac{(b_{ki} - a_{kj})^2}{s_{kj}^2}}, \qquad [1]$$

where a_{ki} and b_{kj} are the 1980–1999 and 2080–2099 means for climate variable k at gridpoints i and j and s_{kj} is the standard deviation of the interannual variability for 1980–1999. Effects of climate model bias are minimized by comparing simulated end-20th- to end-21st-century climates. For local climate change, $i = j$. The SED equally weights all variables and emphasizes 21st-century trends that are large relative to 1980–1999 interannual variability. SED scores are first calculated for each global climate model and then averaged into the ensembles reported here.

Four climate variables are used: mean surface air temperature and precipitation for June–August (JJA) and December–February (DJF). These variables were chosen because (*i*) they represent controls of seasonal temperature and moisture availability on plant distributions and abundance (32), (*ii*) seasonal means are robust features of model simulations, and (*iii*) they are compatible with prior work linking the occurrence of past no-analog plant communities (12) to no-analog climates (11). These variables correlate well with other proposed bioclimatic controls on species distributions (e.g., growing degree days, actual and potential transpiration, and minimum and maximum annual temperature) (33, 34). For example, linear regression models using 1961–1990 mean monthly data from the Climate Research Unit TS2.1 data set (35) and the explanatory variables JJA temperature (TJJA) and DJF temperature (TDJF) explain 93% of the global variance growing degree days. Similarly, linear models using TJJA, TDJF, JJA precipitation (PJJA), and DJF precipitation (PDJF) explain 45% of the global variance in the moisture index α, calculated as the ratio of actual to potential evapotranspiration (32). We opted not to include metrics of 21st-century variability or the frequency of extreme events because projected trends in 21st-century climate variability are more uncertain than changes in means.

Local climate change is measured as the SED between 20th- and 21st-century realizations for each gridpoint (Fig. 2 *A* and *B*). High SED scores correspond to larger local climate change and integrate changes in temperature and precipitation. Novel terrestrial climates are identified by comparing the 21st-century climate realization for each land gridpoint to the 20th-century climate realizations for all land gridpoints and retaining the minimum SED (SED$_{min}$). SED$_{min}$ will be equal to or less than the indices of local climate change (Fig. 2, compare *A* and *B* with *C* and *D*). The pool of potential climatic analogs is global, so that high SED$_{min}$ indicate 21st-century climates with no good analog anywhere in 20th-century climate space (Fig. 2 *C* and *D*). Conversely, disappearing climates are identified by comparing each 20th-century gridpoint to all 21st-century climate realiza-

tions and retaining the SED_{min}. High SED_{min} here indicate places where 20th-century climates may disappear; i.e., they have no close counterpart anywhere in the 21st-century simulations (Fig. 2 *E* and *F*).

Although the SED scores usefully summarize multivariate changes in climate, assessing their ecological significance requires placing them in context against known ecological phenomena. We calculate an SED threshold (SED_t) that determines when an SED value is large enough to represent a truly novel climate. A 21st-century gridpoint is defined as novel if its SED_{min} exceeds the threshold. Similarly, a 20th-century climate disappears if its SED_{min} exceeds the threshold.

SED_t is determined by overlaying a global potential vegetation map (36) onto 20th-century climatologies and identifying the SED_t that optimally discriminates between pairs of climate vectors from the same biome vs. pairs of biomes from different biomes (31). SED_t is calculated individually for each biome and then averaged across all biomes (*SI Materials and Methods* and SI Table 2); here we use $SED_t = 3.22$, and in *SI Materials and Methods*, we experiment with a higher threshold ($SED_t = 5.33$) (SI Figs. 5–7). Biomes are global-scale ecosystems whose distributions are climatically controlled (32, 37), making them well suited for determining whether a particular level of climate change (as represented by SED scores) is ecologically significant. SED_t thus represents a temporal climatic change equivalent to the spatial difference in climates among extant biomes, and is a conservative estimator of the extent of novel and disappearing climates. This is because all locations from finer-scale ecological entities tend to have fairly similar climates, and so SED_t will be low, whereas biomes encompass a wider range of climates, and so SED_t will be high. Thus, the climatic differences among biomes are large relative to the climatic differences among finer-scale ecological phenomena, so that a "biome-scale" climate change likely will be significant for finer-scale ecological entities.

Close climatic similarities between geographically distant locations are not relevant for species constrained by dispersal limitations. We therefore conducted a second set of analyses in which the potential pool of climatic analogs is restricted to locations within 500 km (Fig. 3). The 500-km radius is intentionally large [exceeding the highest known rates of plant migration during the last deglaciation ($\approx$200 km per century) (38)], because larger radii produce more conservative identifications of novel and disappearing climates. This analysis affects only the predicted distribution of novel and disappearing climates (Fig. 2 *C–F*), not local change (Fig. 2 *A* and *B*).

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