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The Influence of Late Quaternary Climate-Change Velocity on Species Endemism

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The effects of climate change on biodiversity should depend in part on climate displacement rate (climate-change velocity) and its interaction with species' capacity to migrate. We estimated Late Quaternary glacial-interglacial climate-change velocity by integrating macroclimatic shifts since the Last Glacial Maximum with topoclimatic gradients. Globally, areas with high velocities were associated with marked absences of small-ranged amphibians, mammals, and birds. The association between endemism and velocity was weakest in the highly vagile birds and strongest in the weakly dispersing amphibians, linking dispersal ability to extinction risk due to climate change. High velocity was also associated with low endemism at regional scales, especially in wet and aseasonal regions. Overall, we show that low-velocity areas are essential refuges for Earth's many small-ranged species.

Anthropogenic climate change is a major threat to Earth's biodiversity and the ecosystem services it provides (1). As climate changes, the conditions suitable for local persistence of a particular species move across the surface of the Earth, driving species responses both to recent warming (2–4) and to long-term natural climate cycles (5–8). Species with strong dispersal abilities inhabiting relatively stable climates may track climate fairly closely. Conversely, species with weak dispersal abilities relative to the rate of climate change may fail fully to oc-

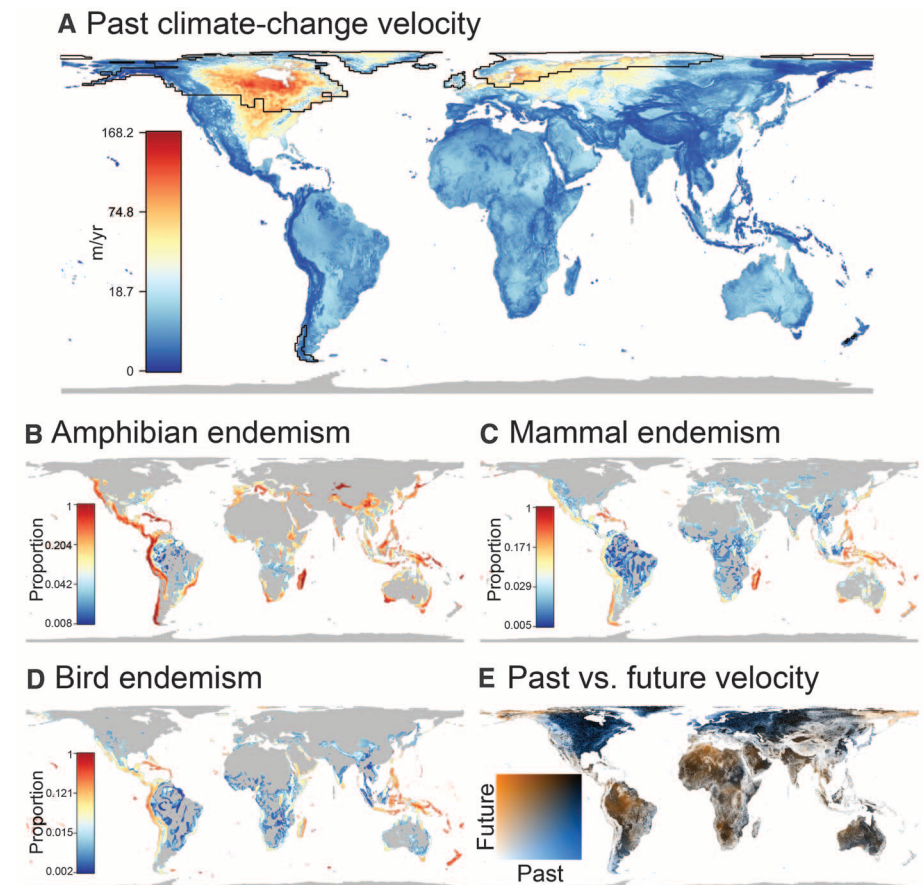
cupy climatically suitable areas (9–14) and may even go extinct, despite appropriate habitat being present elsewhere (15–17).

Climate-change velocity is a measure of the local rate of displacement of climatic conditions over Earth's surface (18). It integrates macroclimatic shifts with local spatial topoclimate gradients and is calculated by dividing the rate of climate change through time by the local rate of climate change across space, yielding a local instantaneous velocity measure. By describing the local rate at which species must migrate to track

changing climate, climate-change velocity is more biologically relevant than are traditional macroclimatic anomalies (13, 16, 19, 20). Furthermore, because climate-change velocity incorporates fine-scale topoclimate gradients it captures the important buffering effect of topographic heterogeneity on climate change (21). For example, a given temperature change should have very different biological consequences depending on topographic context: In flat areas, considerable movement is required to track a 1°C increase in temperature, whereas a short shift uphill could be sufficient in mountains. Thus, species distributed in topographically homogenous landscapes will experience higher climate-change velocities and therefore require stronger dispersal abilities to track climate change than those of species in heterogeneous landscapes.

High climate-change velocities are likely to be associated with incomplete range filling and species extinctions (22). Not all species, however,

Fig. 1. Global maps of (A) climate-change velocity since the Last Glacial Maximum (21,000 years ago); proportional endemism of (B) amphibians, (C) mammals, and (D) birds; and (E) relationships of past and predicted future climate-change velocity. Velocity is highest in northeastern North America and north-central Eurasia; these same areas display low or no endemism (the black line delimits areas that were glaciated at LGM). Mountain ranges and other low-velocity regions exhibit higher endemic richness of amphibians, mammals, and birds. Rank-transformed velocity since the LGM and rank-transformed velocities until 2080 show similar spatial patterns, but there are areas of important mismatch. Orange areas, where velocities in the past have been low but predicted future velocities are expected to be high, are a particular conservation concern.



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are at equal risk from high velocity (20). Strong dispersers should be most able to maintain distributional equilibrium with climate conditions and are therefore likely to occupy more of their potential range and avoid extinction. Species with small ranges are at particular risk of extinction (20); they often have small population sizes and densities (23) and are less likely to occupy refuges that remain suitable during climate oscillations (15, 16, 24). Range size may also reflect other species characteristics that influence resilience to climate fluctuation, with widespread species tending to have broad climatic tolerances (25), generalist strategies (23), and strong dispersal capabilities (23). Hence, high-velocity regions should have fewer small-ranged species and fewer species with poor dispersal ability (16).

To test these hypotheses, we used reconstructions of mean annual temperature at the Last Glacial Maximum (LGM; 21,000 years ago) to calculate a global map of climate-change velocity from the LGM to the present (26) and tested the effects of velocity on patterns of range size and species richness of amphibians, mammals, and birds (27). The difference between the LGM and the present is one of the strongest climatic shifts in all of the Quaternary (28), and its spatial pattern is probably similar to the spatial patterns of earlier climate cycles (16). Our analysis revealed that the LGM-to-present climate-change velocity exhibits marked geographic variation, with peaks in northeastern North America and

north-central Eurasia (Fig. 1A). Velocities tended to be lower in the Southern Hemisphere and in mountainous areas.

Globally, small-ranged (<250,000 km²; hereafter termed “endemic”) amphibians, mammals, and birds are concentrated where climate-change velocity is low (Fig. 1, B to D) [results were not sensitive to the particular definition of small ranges (27)]. In high-velocity northeastern North America and north-central Eurasia, endemic species are nearly absent, whereas low-velocity areas often harbor highly endemic faunas. For all species groups, low-velocity sites are more likely to harbor endemic species than are high-velocity sites (Fig. 2, insets; logistic regression with spatial filters: $n = 2000$ grid cells, all $P < 0.0001$). In addition, among regions ($10^\circ \times 10^\circ$ equivalents) containing at least one endemic species, velocity is strongly and negatively related to the proportion of amphibian [bivariate regression; $n = 188$ regions, coefficient of determination (r^2) = 0.283, $P < 0.001$], mammal ($n = 231$ regions, $r^2 = 0.328$, $P < 0.001$), and bird ($n = 240$ regions, $r^2 = 0.385$, $P < 0.001$) species that are endemic (Fig. 2). We excluded glaciated areas (Fig. 1A) from this analysis, but investigations showed that results were not sensitive to this decision.

It is widely accepted that modern climate influences species distributions and diversity, whereas the role of historical determinants is less clear (23). We therefore examined models that incorporated descriptions of modern climate, the spa-

tial pattern of modern climate conditions, and climate-change velocity. The spatial pattern of modern climate conditions was summarized by calculating, for each grid cell, the total area of land within a 1000-km radius that had a mean annual temperature (MAT) within 1°C and mean annual precipitation (MAP) within 100 mm of that focal cell (24). The extent of analogous modern climate exerted strong influences on endemism, reflecting the fact that regionally rare climates are likely to contain small-ranged species (Table 1) (24). Endemism of all three groups was negatively related to productivity and to two measures of seasonality. In models that considered all variables together while controlling for spatial autocorrelation [simultaneous autoregressive models (SARs)], velocity was a highly significant negative predictor of endemism for all groups, and for the amphibians was second in importance only to the extent of analogous climate. We examined the effect of adding terms to this model to describe the interaction of velocity and modern climate descriptors. Including these terms generally had small effects on other coefficient estimates, and only one such interaction was significant (velocity \times precipitation seasonality for amphibians), so these interactions were not considered further. We examined all subsets of the full SAR models and compared them using Akaike’s Information Criterion (AIC). For all groups, models incorporating velocity were always strongly preferred over equivalent models without velocity (mean AIC improvement: amphibians, 29.6; mammals, 38.5; and birds, 39.0). Across the full model set with and without climate-change velocity, there was high support for velocity as part of the best model (summed Akaike weights for velocity > 0.989 for all groups). These results show that past climate-change velocity and modern climate act together to determine global patterns of endemism.

Because velocity incorporates fine-scale topographic effects on climate stability, it should also contribute to within-region variation in endemism. To test this, we divided the world into regions ($10^\circ \times 10^\circ$ equivalents) and asked whether velocity was correlated with endemism within these regions. For all three species groups, high-velocity areas within regions were associated with low endemism (global means of within-region correlation coefficients: amphibians, $r = -0.160$; mammals, $r = -0.157$; and birds, $r = -0.091$, all $P < 0.01$) (Fig. 3). This overall pattern is consistent with the loss of small-ranged species in high-velocity regions, but the local importance of velocity showed strong geographic variation. Velocity should have the strongest impact where the climate is sometimes highly suitable for a given group, potentially favoring the generation and maintenance of endemic diversity (29). In contrast, regions characterized by generally unfavorable conditions are expected to contain few endemics, whether or not velocity is low. In addition, the ability of species to cope with temperature fluctuations is thought to vary spatially, with species in highly seasonal

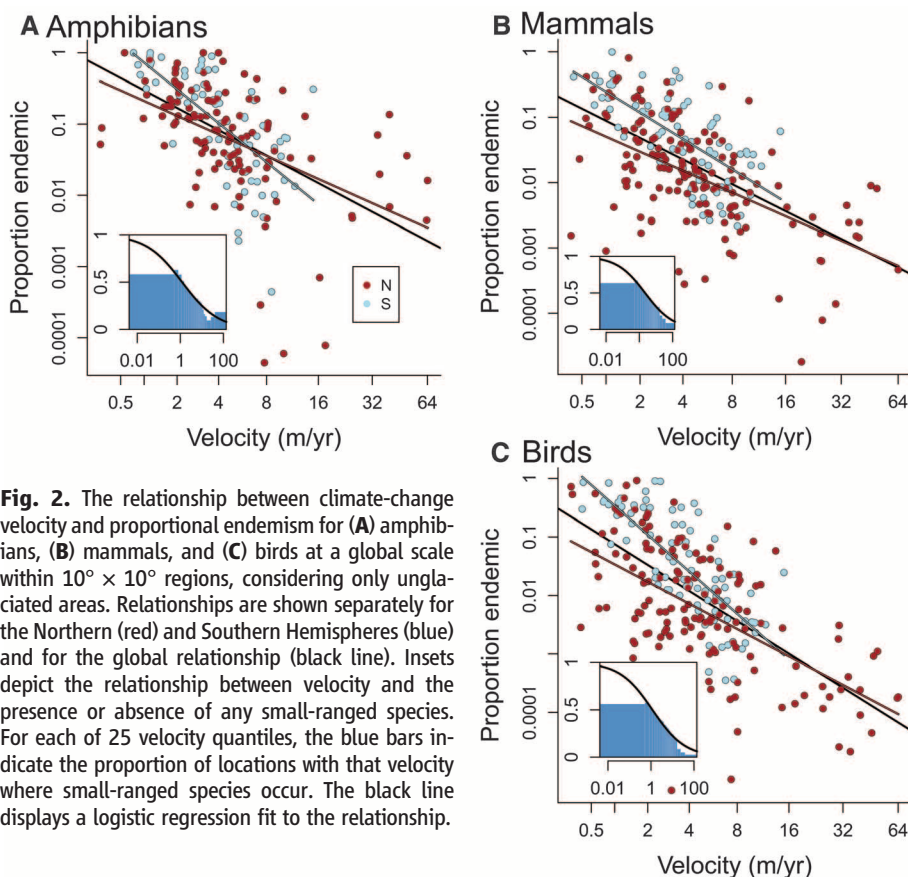


Fig. 2. The relationship between climate-change velocity and proportional endemism for (A) amphibians, (B) mammals, and (C) birds at a global scale within $10^\circ \times 10^\circ$ regions, considering only unglaciated areas. Relationships are shown separately for the Northern (red) and Southern Hemispheres (blue) and for the global relationship (black line). Insets depict the relationship between velocity and the presence or absence of any small-ranged species. For each of 25 velocity quantiles, the blue bars indicate the proportion of locations with that velocity where small-ranged species occur. The black line displays a logistic regression fit to the relationship.

areas tolerating a wider temperature range (30). We tested these hypotheses by identifying the modern climatic variables that most strongly control the within-region correlation of velocity and endemism patterns (table S9). For all three species groups, the models with the lowest AIC scores contained a single significant predictor and were consistent with the above predictions; velocity was particularly important for amphibians and mammals where precipitation was high [amphibians, $n = 125$ regions, standardized regression coefficient (β) = -0.185 , $P = 0.0465$; mammals, $n = 149$ regions, $\beta = -0.259$, $P = 0.0018$] and for birds where temperature seasonality was low ($n = 135$ regions, $\beta = 0.334$, $P = 0.0102$) (Fig. 3).

Although a comprehensive test has thus far been lacking, the importance of climate-change velocity for a group should depend on the dispersal abilities of its species. Hence, of the taxa analyzed, birds should be best at tracking high-velocity changes, whereas amphibians should be worst (9). Indeed, the importance of velocity in determining global patterns of endemism decreased from amphibians (standardized $\beta = -0.288$) to mammals (standardized $\beta = -0.216$) to birds (standardized $\beta = -0.183$) (Table 1). Furthermore, velocity was most tightly correlated with patterns of within-region endemism for amphibians and least correlated for birds. Lending additional support to the importance of dispersal ability, velocity was also more tightly associated with patterns of nonvolant mammal endemism (standardized global $\beta = -0.166$, $P = 0.0058$, mean local $r = -0.165$) than with bat endemism (standardized global $\beta = -0.135$, $P = 0.0670$, mean local $r = -0.034$). Global patterns of endemism were well-correlated among the three groups, suggesting that overall they respond to similar drivers. However, regions with low amphibian endemism relative to avian endemism (which are correlated, $r = 0.681$) tended to have high velocity, indicating that amphibians respond more strongly than do birds to climate change (multiple regression of amphibian endemism against velocity and avian endemism, $n = 183$ regions, standardized $\beta_{\text{velocity}} = -0.281$, $P = 0.0010$). Similar results were obtained for amphibian endemism relative to mammalian endemism ($r = 0.693$, $n = 185$ regions, $\beta_{\text{velocity}} = -0.283$, $P = 0.0010$) and mammalian endemism relative to avian endemism ($r = 0.819$, $n = 212$ regions, $\beta_{\text{velocity}} = -0.175$, $P = 0.0028$). Richness of the lowest three range-size quartiles in amphibians is low relative to the equivalent avian richness ($n = 175$ regions, $\beta_{\text{velocity}} = -0.247$, $P = 0.0031$) and mammal richness ($n = 173$ regions, $\beta_{\text{velocity}} = -0.333$, $P < 0.0001$) in high-velocity regions. As expected given their low dispersal ability, amphibian assemblages in high-velocity regions were thus particularly depauperate of endemic species relative to bird and mammal assemblages.

The focal relationship between velocity and endemism is corroborated by other patterns in the distributions of all three groups. At both global and regional spatial scales, high velocity was associated with larger median range sizes, lower

Table 1. Relationships of seven predictor variables to global patterns of proportional endemism for amphibians, mammals, and birds. GVI, generalized vegetation index; MAT, mean annual temperature; MAP, mean annual precipitation; TS, temperature seasonality; PS, precipitation seasonality; Extent, the regional extent of analogous climate; and Velocity, Late Quaternary climate-change velocity. Five comparative measures were used: the coefficient of determination from bivariate regressions (r^2), standardized regression coefficients estimated from ordinary least-squares multiple regression (OLS), simultaneous autoregressive models using all predictors (SAR), the reduced SAR model with the lowest AIC score (SAR_{reduced}), and Akaike weights based on SAR models. Blank cells indicate variables that were not included in the reduced model. Figures in text are based on the full SAR models, which were most consistently successful at removing residual spatial autocorrelation. The effect of the change in MAT between LGM and present (Anomaly) and topographic heterogeneity (TH) were tested by replacing velocity in all models with each of these variables. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

	r^2	OLS	SAR	SAR _{reduced}	Weight _{AIC}
Amphibians					
GVI	0.227***	-0.185**	-0.196**	-0.198**	0.989
MAT	0.002	0.010	0.008		0.294
MAP	0.090***	-0.125	-0.115	-0.11	0.460
TS	0.068***	-0.018	0.001		0.312
PS	0.073***	-0.233***	-0.244***	-0.241***	0.997
Extent	0.415***	-0.439***	-0.414***	-0.411***	1.000
Velocity	0.283***	-0.252***	-0.288***	-0.289***	1.000
Anomaly	0.082***	-0.203**	-0.213**	-0.207***	0.979
TH	0.134***	0.230**	0.260***	0.285***	0.998
Mammals					
GVI	0.253***	-0.169***	-0.160***	-0.160***	0.993
MAT	0.158***	0.228**	0.216*	0.216*	0.882
MAP	0.203***	-0.215**	-0.190*	-0.190*	0.736
TS	0.313***	-0.180	-0.182	-0.182	0.597
PS	0.039**	-0.194***	-0.173***	-0.173***	0.929
Extent	0.538***	-0.490***	-0.467***	-0.467***	1.000
Velocity	0.328***	-0.199***	-0.216***	-0.216***	0.998
Anomaly	0.187***	-0.155**	-0.158**	-0.158**	0.975
TH	0.023*	0.092	0.106*	0.106*	0.646
Birds					
GVI	0.297***	-0.237***	-0.212***	-0.213***	1.000
MAT	0.102***	0.065	0.021		0.284
MAP	0.137***	-0.317***	-0.303***	-0.302***	0.999
TS	0.348***	-0.500***	-0.549***	-0.565***	1.000
PS	0.036**	-0.183***	-0.120*	-0.114*	0.838
Extent	0.446***	-0.369***	-0.323***	-0.320***	1.000
Velocity	0.385***	-0.194***	-0.183***	-0.180***	0.989
Anomaly	0.222***	-0.148***	-0.121*	-0.119*	0.733
TH	0.015	0.074	0.086*	0.081*	0.726

variation in range size within assemblages, reduced richness of species with range size below the median, and weaker, inconsistent, and sometimes positive relationships for richness of species with larger range sizes (figs. S1 to S6 and tables S1 to S6 and S9).

High velocities have been proposed to be associated with incomplete range filling and species extinctions (10, 17, 22). Although we found no evidence for reduced range sizes with higher velocities, the decline in endemism and inferred importance of dispersal ability are consistent with the extinctions hypothesis. However, it may be that velocity per se is not driving endemism but simply correlates with other variables that do have a direct mechanistic link. Alternatively, a direct mechanistic link between velocity and endemism may not require species extinctions. We considered several such alternative hypotheses and show that none are consistent with the data.

High-velocity areas may coincide with those where analogous climate conditions have most expanded since the LGM; low endemism in these areas may occur because species in such areas have expanded their range size accordingly. Climate expansion since the LGM was highly correlated with the extent of modern analogous conditions ($r = 0.794$) but was a weaker predictor of endemism in all cases (compare Table 1 with table S12). Furthermore, the range expansion hypothesis predicts that the groups with strongest dispersal ability (birds) should have expanded their ranges most and therefore should show the strongest relationships to velocity, which is contrary to our results. It is also possible that velocity appears to be an important predictor, not because of a mechanistic link but only because it is derived from another variable that does have a direct link. However, climate-change velocity was a better predictor than either of its components

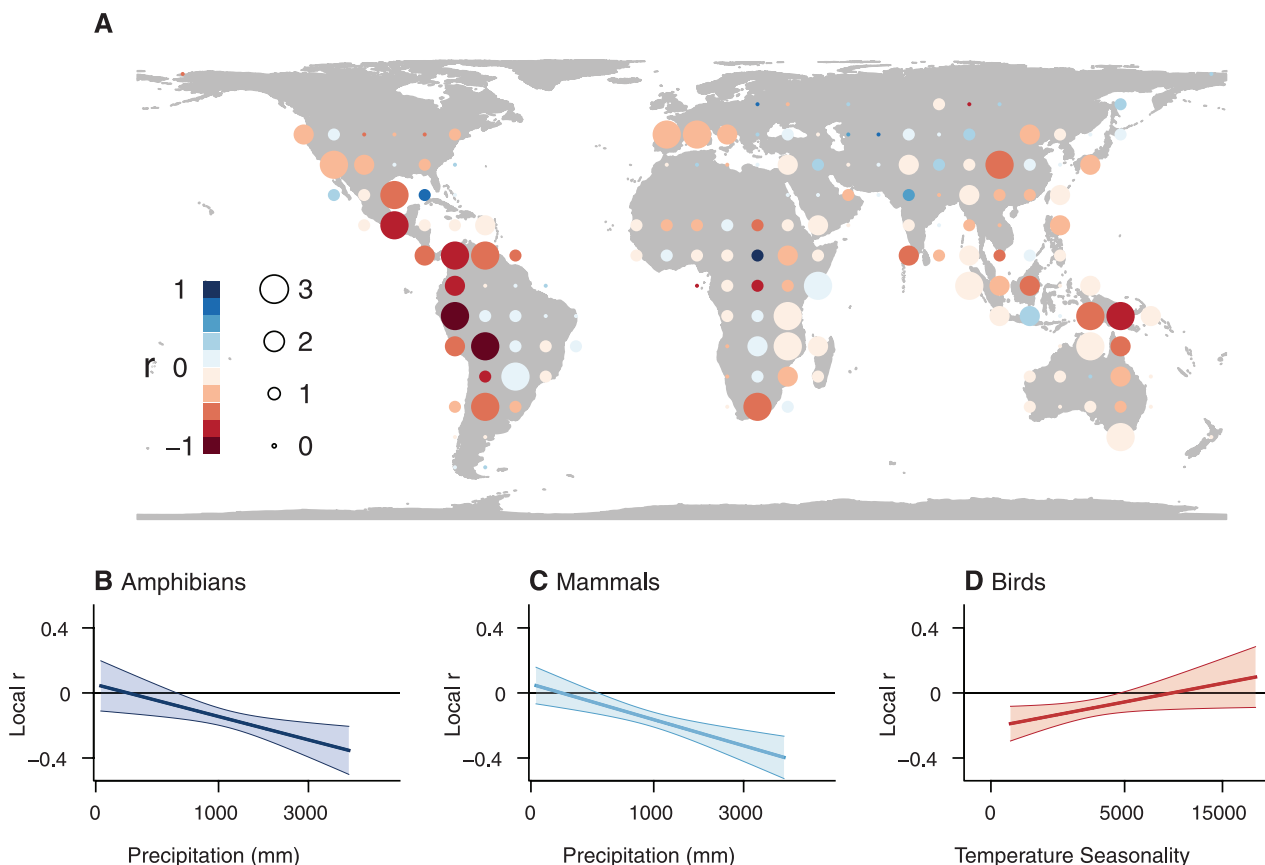


Fig. 3. The global pattern of within-region fit of climate-change velocity to patterns of endemism. **(A)** Within each $10^\circ \times 10^\circ$ region, circle size indicates the number of species groups for which velocity was significantly ($P < 0.05$) associated with endemism. The color of the circle corresponds to the mean correlation

coefficient across all groups present within that region. **(B to D)** Globally, strong within-region correlations between velocity and endemism were associated with high precipitation (amphibians and mammals) and low temperature seasonality (birds). Envelopes around each line show the 90% confidence interval.

(topographic heterogeneity and macroclimate anomaly) and was the only one with consistent predictive power across scales (Table 1), which suggests that topographic heterogeneity and anomaly both contain important and complementary information. High endemism and low velocity occur not only in mountains but also in macroclimatically stable, relatively flat regions (such as portions of the Amazon basin and central Africa). At the same time, high-velocity mountain areas harbor low endemism (such as the Altai mountains of northern Mongolia and some mountains in the western United States).

Does a direct role of velocity depend on extinctions, and are alternatives consistent with the data? Dynesius and Jansson (15) proposed three interrelated mechanisms linking climate stability and patterns of richness and range size: (i) Instability may select for increased dispersal ability and generalism, leading to large ranges; (ii) gradual speciation rates may be reduced in unstable areas, producing a lack of young, small-ranged species; and (iii) small-ranged species may have gone extinct in unstable areas. Underlying all of these hypotheses is the process of lineage extinction across a range of evolutionary scales, from selection acting on within-species lineages to the extinction of newly diverging or full species (31). In principal, reduced speciation rates [explana-

tion (ii)] might instead be due to high rates of gene flow among populations in unstable, shifting climates. However, this mixing should be most pronounced for strongly dispersing species. In contrast, lineage extinctions at all levels should have the strongest effects on weak dispersers, which is consistent with our results. Thus, elevated extinction rates—likely across a range of evolutionary scales (31)—appear to best explain the association of low endemism with high velocity (17, 22).

Our results have important implications for conservation in a world that is increasingly experiencing elevated climate-change velocities (18). Areas that have experienced high velocities in the past are on average also expected to experience high velocities over the next century (Fig. 1E and fig. S7). As we have shown, these areas are already missing small-ranged species, suggesting that most of the remaining species may cope well with future changes. However, there are important mismatches between the spatial patterns of past and future climate change; areas with low velocities in the past, high concentrations of endemic species, and high velocities into the future are a particular conservation concern. These areas include western Amazonia, where concentrations of endemic species that have experienced relatively low-velocity changes in the past may be faced with rapid climate shifts in the near future.

Taken together, these results indicate that past climate changes have left important legacies in contemporary range size and species richness patterns, supplemented by the influences of modern climate and its spatial pattern. Small-ranged species constitute most of Earth's species diversity (23); our findings show that these species, especially those from less vagile groups, are sensitive to climate movements and are concentrated in areas where possibilities for tracking past climate changes have been greatest. This conclusion also suggests that small-ranged, weakly dispersing species in previously stable regions experiencing high future climate-change velocities will be at greatest extinction risk from anthropogenic climate change.

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- Acknowledgments:** We thank the Aarhus University Research Foundation for financial support. This study was also supported in part by MADALGO—Center for Massive Data Algorithmics, a Center of the Danish National Research Foundation. B.D. is supported by the Danish Council for Independent Research—Natural Sciences, and W.J.S. is funded by Arcadia. We thank international climate modeling groups for providing their data for analysis, the Laboratoire des Sciences du Climat et de l'Environnement

for collecting and archiving the paleoclimate model data, the International Union for Conservation of Nature and Natural Resources for making the amphibian and mammal range data available, and the Natural Environment Research Council-funded Avian Diversity Hotspots Consortium (NER/O/S/2001/01230) for the use of the bird range data. We thank four anonymous reviewers whose constructive comments improved this manuscript. Data are archived at Dryad (<http://dx.doi.org/10.5061/dryad.b13j1>).

Supporting Online Material

www.sciencemag.org/cgi/content/full/science.1210173/DC1
 Materials and Methods
 Figs. S1 to S12
 Tables S1 to S12
 References (32–54)

22 June 2011; accepted 19 August 2011
 Published online 6 October 2011;
 10.1126/science.1210173

Long-Term Change in the Nitrogen Cycle of Tropical Forests

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Deposition of reactive nitrogen (N) from human activities has large effects on temperate forests where low natural N availability limits productivity but is not known to affect tropical forests where natural N availability is often much greater. Leaf N and the ratio of N isotopes ($\delta^{15}\text{N}$) increased substantially in a moist forest in Panama between ~1968 and 2007, as did tree-ring $\delta^{15}\text{N}$ in a dry forest in Thailand over the past century. A decade of fertilization of a nearby Panamanian forest with N caused similar increases in leaf N and $\delta^{15}\text{N}$. Therefore, our results indicate regional increases in N availability due to anthropogenic N deposition. Atmospheric nitrogen dioxide measurements and increased emissions of anthropogenic reactive N over tropical land areas suggest that these changes are widespread in tropical forests.

Anthropogenic N fixation has approximately doubled atmospheric deposition of reactive N in terrestrial ecosystems globally, with regional variation resulting from differences in the intensity of agriculture, the burning of fossil fuels, and biomass burning (1). Many temperate and boreal ecosystems are N limited; in these regions, atmospheric N deposition has caused the acidification of soils and waters, loss of soil cations, a switch from N to P limitation, a decline in the diversity of plant communities adapted to low N availability, and increases in carbon uptake and storage (2, 3). Natural N availability is much greater in many tropical forests than in most temperate forests due to high rates of N fixation by heterotrophic soil microbes

and rhizobia associated with legumes, which are abundant in many tropical forests (4). Nitrogen deposition is increasing in the tropics, and this region may see the most dramatic increases in the coming decades (1). It has been hypothesized that this will acidify soils, deplete soil nutrients, reduce tree growth and carbon storage, and negatively affect biodiversity in tropical forests (5, 6). Yet despite extensive speculation, there remains no direct evidence for changes in the N cycle in tropical forests.

The ratio of stable N isotopes ($\delta^{15}\text{N}$) reflects the nature of the N cycle in ecosystems, with higher values indicating greater N availability and a more open N cycle (7, 8). In temperate ecosystems where N deposition is low, leaf N concentrations and the $\delta^{15}\text{N}$ of leaves and wood decreased during the 20th century, indicating progressive N limitation in response to changes in land use (9) and increasing atmospheric CO_2 concentrations (10). In contrast, wood $\delta^{15}\text{N}$ values have increased in temperate forests with high rates of N deposition or a history of recent disturbance, suggesting more open N cycles under such conditions (11, 12).

We compared leaves from herbarium specimens (158 species) collected ~40 years ago (~1968) from a tropical moist forest on Barro

Colorado Island (BCI), Republic of Panama, with sun and shade leaves (340 species) collected in 2007. Over four decades, leaf $\delta^{15}\text{N}$ increases averaged 1.4 ± 0.16 per mil (‰) (SEM) and $2.6 \pm 0.1\%$ when comparing 1960s leaves to conspecific 2007 shade and sun leaves, respectively. Based on their leaf mass per area, 1960s leaves included a mixture of both sun and shade leaves (13). The increase in leaf $\delta^{15}\text{N}$ occurred in both legumes (Fabaceae) and nonlegumes (Fig. 1, A and B). Foliar N concentrations in nonlegumes increased by $7.7 \pm 1.9\%$ and $15.2 \pm 2.5\%$ when comparing 1960s leaves to 2007 sun and shade leaves, respectively (Fig. 1C). Legumes had substantially greater foliar N concentrations than nonlegumes, and there was no overall change in their foliar N concentration between the 1960s and 2007 (Fig. 1D).

To assess whether the changes detected on BCI are representative of tropical forests more broadly, we determined $\delta^{15}\text{N}$ in tree rings from three nonleguminous tree species in the Huai Kha Khaeng Reserve, a remote monsoon forest near the Thailand-Myanmar border. Significant increases in $\delta^{15}\text{N}$ during the past century were detected in all three species (Fig. 2). Similar changes were reported previously for tree rings in two Amazonian rainforest tree species (14).

A forest N addition experiment conducted 1 km from BCI provides perspective on the changes in foliar N composition (15). Foliar $\delta^{15}\text{N}$ increased by 0.3 to 1.5‰ in four tree species and by ~0.5 to 1.2‰ in fine litter (15), and the N concentration in litterfall increased by 7% (16) after 8 to 9 years of fertilization with 125 kg N $\text{ha}^{-1}\text{year}^{-1}$. The observed increase in leaf $\delta^{15}\text{N}$ did not reflect the signal of the N fertilizer, which had a lower $\delta^{15}\text{N}$ (–2.2‰) than leaves of nonfertilized trees in control plots (15) and therefore should have resulted in a decline rather than an increase in foliar $\delta^{15}\text{N}$. Nitrogen fertilization also increased NO_3 leaching (from 0.01 to 0.93 mg N liter^{–1}), NO flux (from 70 to 196 $\mu\text{g N m}^{-2}\text{day}^{-1}$), and N_2O flux (from 448 to 1498 $\mu\text{g N m}^{-2}\text{day}^{-1}$) (15), confirming that the increase in leaf $\delta^{15}\text{N}$ after N fertilization was associated with a more

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