

This suggests predictive limits of our approach, in that more-connected systems with more soil evaporation and less-connected systems with less soil evaporation will produce similar continental output flux isotope ratios.

The terrestrial hydrologic partitioning estimated here corresponds to a total transpiration of  $55,000 \pm 12,000 \text{ km}^3$  per year (mean  $\pm 1$  SD), a total soil evaporation of  $5000 \pm 4000 \text{ km}^3$  per year, and a total surface water evaporation of  $2000 \pm 2000 \text{ km}^3$  per year, assuming an interception of  $23,000 \pm 10,000 \text{ km}^3$  per year (27) and a continental precipitation of  $115,000 \pm 2000 \text{ km}^3$  per year (28) (Fig. 3). The transpired fraction determined here is consistent with previous meta-analyses (Fig. 1C) and places an observational constraint on transpiration estimates from global Earth system models, which range between 38 and 80% (4–6, 29). The fraction of total evapotranspiration flux occurring from surface waters, 2.9%, is also consistent with values from global Earth system models, which range from 2 to 4% when reported (29). Globally, tropical forests provide the bulk of continental transpiration, although these regions contribute modest amounts of soil and surface water evaporation as well.

Transpiration fluxes form the primary link between the water and carbon cycles, with water lost from plant stomata during carbon assimilation (i.e., plant water use efficiency) being a critical factor determining ecosystem function and productivity. Although we estimate that plant transpiration is a majority of the evapotranspiration flux, our results demonstrate that previous partitioning approaches may overestimate the contribution of transpiration, because they do not consider evaporation from multiple catchment water pools and their connectivity. Furthermore, isotopic partitioning approaches are sensitive to bulk flux estimates and their uncertainties, as well as assumptions about interception rates, with larger interception isotopically indistinguishable from increased transpiration because both fluxes are often assumed to be unfractionated relative to their source waters (6, 20). Because a majority of evaporation occurs from soils and not open waters, more knowledge is needed of the role of ecosystem structure and microclimate in determining sub-canopy evaporation rates.

Finally, the partial hydrologic disconnect between bound and mobile waters, which our estimates suggest is substantial and pervasive at the global scale, has implications for prediction and monitoring of both water quantity and quality within streams and rivers. The hydrologic and hydrochemical properties of surface water systems are strongly influenced by physical flow paths within the near surface, and the low connectivity found here suggests, for example, that stream biogeochemistry may be less sensitive to soil zone processes than it would be if hydrologic connectivity were higher. Although we determined a single average connectivity value, connectivity varies with geography and in time as preferential flow paths are activated and deactivated throughout the year (30). Indeed, the relation between the

connectivity metric and soil-water transit time distributions is likely to be complex. Given the ubiquitous nature of both water quantity and water quality issues affecting watersheds worldwide, an improved understanding of hydrologic connectivity at variety of temporal and spatial scales is essential.

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#### SUPPLEMENTARY MATERIALS

[www.sciencemag.org/content/349/6244/175/suppl/DC1](http://www.sciencemag.org/content/349/6244/175/suppl/DC1)  
Materials and Methods  
Figs. S1 to S3  
References (31–37)

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#### CLIMATE CHANGE

## Climate change impacts on bumblebees converge across continents

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For many species, geographical ranges are expanding toward the poles in response to climate change, while remaining stable along range edges nearest the equator. Using long-term observations across Europe and North America over 110 years, we tested for climate change–related range shifts in bumblebee species across the full extents of their latitudinal and thermal limits and movements along elevation gradients. We found cross-continently consistent trends in failures to track warming through time at species' northern range limits, range losses from southern range limits, and shifts to higher elevations among southern species. These effects are independent of changing land uses or pesticide applications and underscore the need to test for climate impacts at both leading and trailing latitudinal and thermal limits for species.

**B**iological effects of climate change threaten many species (1), necessitating advances in techniques to assess their vulnerabilities (2). In addition to shifts in the timing of species' life cycles, warming has caused

range expansion toward the poles and higher elevations (3–6). Climate impacts could cause losses from parts of species' trailing range margins (7), but those losses are infrequently observed (4). Such responses depend on species' traits, such as

heat or cold tolerance, that reflect shared evolutionary history and climatic origins (e.g., tropical or temperate) of taxa (8, 9). Climate change can interact with other threats, like land-use intensification, to alter species' responses to emerging conditions (10). Such global changes can alter or erode ecological services provided by the affected species (11). Few species assemblages contribute more to these services than bumblebees (*Bombus*), many of which are declining (12, 13). No study has yet evaluated climate change impacts across the latitudinal and thermal limits of such a large species assemblage spanning two continents.

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We assembled a database of ~423,000 georeferenced observations for 67 European and North American bumblebee species (fig. S1 and tables S1 and S2). Species observations were gathered from the Global Biodiversity Information Facility (171,479 North American and 192,039 European records) (14), *Bumblebees of North America* (15) (153,023 records), and the Status and Trends of European Pollinators Collaborative Project (237,586 records). We measured differences in species' northern and southern range limits, the warmest or coolest temperatures occupied, and their mean elevations in three periods (1975 to 1986, 1987 to 1998, and 1999 to 2010) (figs. S2 to S4) relative to a baseline period (1901 to 1974) (16). We investigated whether land use affected these results. Finally, we used high-resolution pesticide application data available in the United States after 1991 to investigate whether total pesticide or neonicotinoid applications accounted for changes in bumblebee species' range or thermal limits (table S3). Tests used phylogenetic generalized least-squares models (PGLS), using a phylogenetic tree constructed from nuclear and mitochondrial markers (17), and accounted for differences in sampling intensity between time periods (Table 1).

If species expanded their northern range limits to track recent warming, their ranges should show positive (northward) latitudinal shifts, but cool thermal limits should be stable through time. In contrast to expectations and responses known from other taxa (4), there has been no change in

the northern limits of bumblebee distributions in North America or Europe (Fig. 1A). Despite substantial warming (~ +2.5°C), bumblebee species have also failed to track warming along their cool thermal limits on both continents (Fig. 1B and Table 1). These failures to track climate change occur in parallel in regions that differ in their intensities of human land use (e.g., Canada and northern Europe), which had no direct or interaction-based effect in any statistical model (Table 1).

If bumblebee species climate responses resemble most terrestrial ectotherm taxa (4), their southern range limits should have remained stable with increasing temperatures along species' warm thermal limits. However, bumblebee species' range losses from their historical southern limits have been pronounced in both Europe and North America, with losses growing to ~300 km in southern areas on both continents (Fig. 1C). Throughout North America, species also experienced range losses from the warmest areas they historically occupied, while European species' range losses extend across the warmest regions (where mean temperatures exceed ~15°C) (Fig. 1D). These responses showed a significant phylogenetic signal, with closely related bumblebee species showing increasingly similar range shifts from southern and warm thermal limits (Table 1). As with failures to expand northward or into cooler areas, land-use changes do not relate to range losses from bumblebee species' southern or warm thermal limits.

**Table 1. PGLS models showing climate change and interactive effects on North American and European bumblebees.** Changes in latitude (km north of equator), thermal (°C), or elevation (m) variables observed by 1999 to 2010 for each species (relative to the 1901 to 1974 baseline period) are regressed against predictors listed on the left. Models reported in each column were selected using AIC, which can include statistically nonsignificant

variables. Sample sizes in each time period (median *n* per species = 536) were tested but excluded using AIC. Variable coefficients are given, with SEs in parentheses. A dash indicates that this variable was not part of the AIC-selected model. Ordinary least squares (OLS) regression summary statistics (adjusted *R*<sup>2</sup>) are provided to enable comparison with PGLS results; OLS coefficients are similar.

Predictors	Latitude		Thermal		Elevation
	Northern	Southern	Cool	Warm	
Intercept	−268.3 (614.7)	657.8 (150.4)	2.436 (0.5)	657.8 (150.4)	1075 (340.7)
Latitudinal or thermal limit (1901–1974)	0.04 (0.08)	−0.12 (0.04)	−0.009 (0.05)	0.19 (0.1)	–
Mean latitude (1999–2010)	–	–	–	–	−0.21 (0.07)
Covariates					
Continent	1158 (1039)	–	–	10.59 (2.24)	384.5 (504.1)
Δ Crop land (1999–2010)	−4.25 (7.68)	–	–	–	–
Δ Pasture (1999–2010)	−43.1 (60.71)	–	–	–	–
Interactions with continent					
Thermal or latitudinal limits (1901–1974)	−0.12 (0.14)	–	–	−0.47 (0.12)	–
Δ Crop land (1999–2010)	−9.38 (41.73)	–	–	–	–
Δ Pasture (1999–2010)	74.95 (74.35)	–	–	–	–
Mean latitude (1999–2010)	–	–	–	–	−0.03 (0.1)
Models of trait evolution					
AIC (Independent)	915.5	863.2	291.3	274.5	863.6
AIC (Brownian motion)	962.4	897.4	339.3	293.9	916.4
AIC (Ornstein-Uhlenbeck)	917.5	861.8	293.3	264.9	865.4
AIC (Pagel)	915.3	862.2	293.1	273	860.8
Pagel's λ	−0.15	0.49	0.04	0.64	−0.1
Equivalent OLS regression summary statistics					
Adjusted <i>R</i> <sup>2</sup>	0.15	0.14	−0.01	0.30	0.28

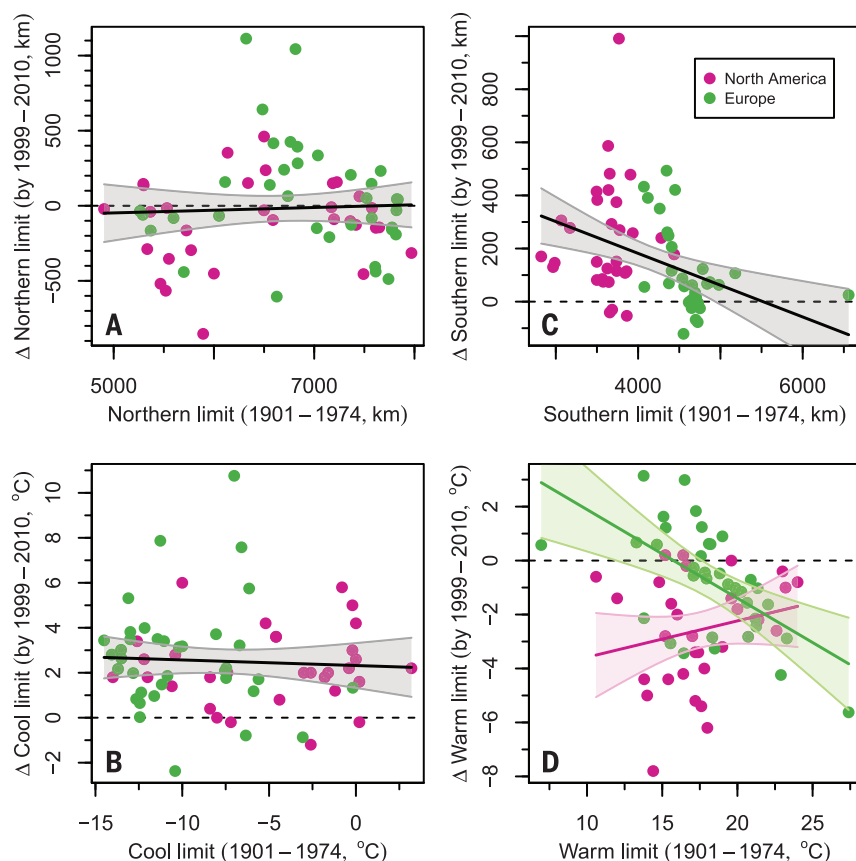
Species with southern geographical ranges retreated to higher elevations across Europe and North America (Table 1 and Fig. 2), consistent with observations of range losses from their southern range limits. Elevation shifts are larger in Europe [i.e., Akaike's information criterion (AIC)-based model selection includes a small continental effect; intercept for Europe, 1459 m (366 SE); North America, 1074 m (340 SE) (Fig. 2)]. Europe's mountainous areas are oriented predominantly east-west, potentially inducing more pronounced upslope shifts. Mean elevations of observations for southern species have risen ~300 m since 1974. Observed shifts along elevation gradients vary considerably among species (3) but follow a coherent geographical pattern. Mean elevations among northern species in Europe and North America shifted lower. Over recent decades, alpine tree lines have advanced upslope in response to human activities, geomorphological factors, and warming (18), potentially overtaking nesting, overwintering, and forage habitats in historically open areas. High-elevation hab-

itat changes could contribute to generalist pollinator declines in mountainous areas (19), particularly among bumblebee species whose ranges have not expanded from their cold thermal limits.

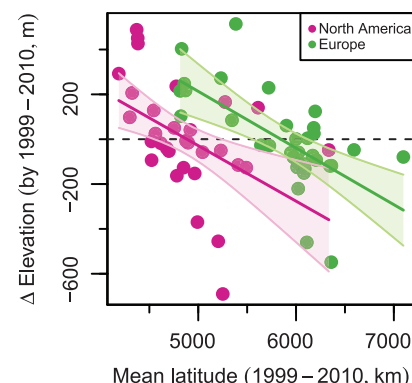
In addition to land-use changes, we investigated whether pesticide use affected shifts in thermal and latitudinal range limits among bumblebees. Spatially detailed, annual pesticide measurements, including neonicotinoid insecticides, were available for the United States after 1991. Neither total pesticide nor neonicotinoid applications there relate to observed shifts in bumblebee species' historical ranges or thermal limits (table S1). Neonicotinoid effects known from individual and colony levels certainly contribute to pollinator declines and could degrade local pollination services. Neonicotinoid effects on bumblebees have been demonstrated experimentally using field-realistic treatments (20). These locally important effects do not "scale up" to explain cross-continental shifts along bumblebee species' thermal or latitudinal limits. The timing of climate change-related shifts

among bumblebee species underscores this observation: Range losses from species' southern limits and failures to track warming conditions began before widespread use of neonicotinoid pesticides (figs. S2 and S3).

Regional analyses suggest that latitudinal range shifts toward the poles are accelerating in most species groups (3), while their trailing range margins remain relatively stable (4). Assemblages showing pronounced northward range expansions and limited southern-range losses, like butterflies, originated and diversified in tropical climates and retain ancestral tolerances to warmer conditions (21). Those species' warming-related extinction risks in temperate environments are low (8) but increase toward warmer areas where climatic conditions resemble those under which they evolved (7, 22). Drawing on comprehensive range data, bumblebee species show opposite range responses across continents relative to most terrestrial assemblages (4): rapid losses from the south and lagging range expansions in the north. Mechanisms leading to observed lags in range responses at species' northern or cool thermal limits require urgent evaluation. Colonization of previously unoccupied areas and maintenance of new populations strongly affect whether species track shifting climatic conditions (23), capacities that appear insufficient among bumblebees. Observed losses from species' southern or warm boundaries in Europe and North America, and associated phylogenetic signals, are consistent with ancestral limitations of bumblebees' warm thermal tolerances and evolutionary origins in cool Palearctic conditions (24). Warming-related extreme events cause bumblebee population losses (25) by imposing demands for energetically costly behavioral thermoregulation, even at high latitudes and elevations (26). Such effects are not yet observed for European bumblebees in cooler regions, where species generally experience temperatures exceeding those observed historically within their ranges (Fig. 1D) (10). Range losses there will likely accelerate without mitigation from climatic refugia (27).



**Fig. 1. Climate change responses of 67 bumblebee species across full latitudinal and thermal limits in Europe and North America.** For each measurement, the y axis shows differences in the latitude of species' range limits [(A) Northern, (C) Southern] or thermal limits [(B) Cool; (D) Warm], respectively, by 1999 to 2010 relative to baseline conditions for 1901 to 1974. Each point represents the mean of five observations at the latitudinal or thermal limits for one bumblebee species (green circles for Europe and pink for North America). Null expectations (dashed lines) are for no temporal change in latitudinal or thermal limits. Range expansions from species' historical northern limits (A) are indicated by positive values, and positive values indicate range losses from species' southern limits (B). Temperature changes show whether bumblebee species are tracking differences along their thermal limits through time (no change), falling behind (positive values), or retreating more rapidly than mean conditions detect (negative values). Confidence bands (95%) for regression models (i.e., with and without continent + interaction against latitudinal or thermal change terms) with the lowest AIC are shown.



**Fig. 2. Change in elevation of 67 bumblebee species by 1999 to 2010 relative to their mean latitude.** Elevations are calculated using mean elevations across species observations. The slopes are similar between continents (according to regression and PGLS analyses). The confidence bands (95%) of regression slopes are shown.



Climate change appears to contribute distinctively, and consistently, to accumulating range compression among bumblebee species across continents. Experimental relocation of bumblebee colonies into new areas could mitigate these range losses. Assessments of climate change on species' ranges need to account for observations across the full extent of species' latitudinal and thermal limits and explicitly test for interactions with other global change drivers.

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## SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/349/6244/177/suppl/DC1  
Materials and Methods  
Supplementary Text  
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Figs. S1 to S4  
Tables S1 to S3  
References (28–55)

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## PLACE CELLS

# Autoassociative dynamics in the generation of sequences of hippocampal place cells

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Neuronal circuits produce self-sustaining sequences of activity patterns, but the precise mechanisms remain unknown. Here we provide evidence for autoassociative dynamics in sequence generation. During sharp-wave ripple (SWR) events, hippocampal neurons express sequenced reactivations, which we show are composed of discrete attractors. Each attractor corresponds to a single location, the representation of which sharpens over the course of several milliseconds, as the reactivation focuses at that location. Subsequently, the reactivation transitions rapidly to a spatially discontinuous location. This alternation between sharpening and transition occurs repeatedly within individual SWRs and is locked to the slow-gamma (25 to 50 hertz) rhythm. These findings support theoretical notions of neural network function and reveal a fundamental discretization in the retrieval of memory in the hippocampus, together with a function for gamma oscillations in the control of attractor dynamics.

In the well-known Hopfield model, a network of recurrently excitable neurons stores discrete memories as stable activity patterns (attractors) to which partial patterns are guaranteed to converge, based on synaptic weights reflecting correlations between neurons in the same pattern (“autoassociation”) (7). Sequences of patterns can also be stored, based on weights reflecting correlations between different patterns (“heteroassociation”), but are generally unsustainable because any noise leads to divergence in subsequent patterns. A solution is to combine fast autoassociation for each pattern with slower heteroassociation for successive patterns, allowing each pattern to be corrected via attractor network dynamics before transitioning to the next pattern in the sequence (2, 3). This process should result in “jumpy” sequences that sharpen individual pattern representations before transitioning to successive patterns; however, direct evidence is lacking, due largely to the difficulty of obtaining data from very large ensembles of neurons expressing internally generated sequences recorded at the time resolution of neuronal dynamics.

Hippocampal SWR-associated place-cell sequences (4–10), often termed “replay,” are a unique experimental model in which neurons with well-defined receptive fields are activated outside those receptive fields and in specific temporal sequences corresponding to physical trajectories through space, all while the animal is stationary, and thus in the absence of corresponding sequences of stimuli or behaviors. We recently developed methods to record simultaneously from very large num-

bers of hippocampal neurons (up to 263) with place fields in a single environment (10), and we applied these recording techniques to examine the fine structure of SWR-associated place-cell sequences to investigate the underlying mechanisms of this form of memory expression and explore the circuit-level dynamics of an attractor system in vivo.

We recorded bilateral ensemble activity from dorsal hippocampal neurons (figs. S1 and S2) of five rat subjects across multiple recording sessions as they explored open arenas or linear tracks (Fig. 1, A, B, G, and H). We obtained simultaneous recordings from large populations of hippocampal neurons in each recording session (80 to 263 units per session; mean  $\pm$  SEM = 159.2  $\pm$  11.8 units per session), allowing us to accurately decode spatial information from the hippocampal ensemble activity patterns using a memory-less, uniform-prior Bayesian decoding algorithm (fig. S3) (5, 10). We identified SWRs that encoded temporally compressed spatial trajectories through the current environment (Fig. 1, C to F and I to L, and fig. S4) (10), which we term “trajectory events” rather than “replay” to reflect the observation that SWRs do not always represent a perfect replay of immediately prior behavior but instead reflect a more broad array of spatial paths (8–10). Across all sessions in the open field and linear track, we identified 815 and 564 SWR events, respectively, that met our criteria to be classified as trajectory events.

Consistent with prior reports (5), trajectory events displayed average velocities in a relatively narrow range (Fig. 2A); however, when we examined trajectory events on a finer time scale, we observed discontinuous trajectories, alternating between immobility (in which consecutive decoding frames represented the same location) and rapid movement (in which consecutive frames represented a sequential path of unique positions; fig.

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## Climate change impacts on bumblebees converge across continents

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### Bucking the trend

Responses to climate change have been observed across many species. There is a general trend for species to shift their ranges poleward or up in elevation. Not all species, however, can make such shifts, and these species might experience more rapid declines. Kerr *et al.* looked at data on bumblebees across North America and Europe over the past 110 years. Bumblebees have not shifted northward and are experiencing shrinking distributions in the southern ends of their range. Such failures to shift may be because of their origins in a cooler climate, and suggest an elevated susceptibility to rapid climate change.

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