nature climate change

Brief Communication

https://doi.org/10.1038/s41558-023-01794-2

Upslope migration is slower in insects that depend on metabolically demanding flight

Received: 5 May 2023

Accepted: 3 August 2023

Published online: 11 September 2023

Check for updates

Michael P. Moore [1] ✉, Jesse Shaich [1] & James T. Stroud [2,3]

Climate change is forcing species to migrate to cooler temperatures at higher elevations, yet many taxa are dispersing slower than necessary. One yet-to-be-tested explanation for inadequate migration rates is that high-elevation environments pose physiological barriers to dispersal, particularly in species with high metabolic demands. By synthesizing across >800 species, we find evidence for metabolic constraints: upslope migration is slower in insects that rely on nature's most expensive locomotor strategy—flight.

Human-mediated climate change is saddling organisms with rising air temperatures, declining precipitation and intensifying swings in daily weather patterns[1]. Although species have genetically adapted to major climatic shifts over long historical timescales[2–4], the rapidity and variability of the current changes make adaptation difficult, particularly since climate change is just one of many anthropogenic threats that must be overcome[2]. To avoid extinction in the face of contemporary climate change, many species are shifting their ranges towards cooler regions at higher latitudes and elevations[4]. However, recent studies have highlighted that the rate of global warming is dramatically outpacing the rate of upslope migration in most cases—even for species with exceptional dispersal abilities such as flight[5,6]. Understanding the mechanisms that facilitate or stifle upslope migration is therefore essential to forecasting species' responses to contemporary climate change and to assessing which taxa may be most vulnerable in the coming years[7–10].

Since elevational gradients present an unusual combination of physiological challenges, physiological limitations could be one strong barrier to upslope migration[11]. For example, higher elevations supply less oxygen for aerobic metabolism owing to lower atmospheric pressure. Animals with high aerobic demands may therefore have difficulty migrating upslope to elevations where their metabolic requirements approach or exceed the supply of oxygen[11,12]. Under this hypothesis, metabolic constraints should be especially acute for species that employ expensive behaviours or forms of locomotion, such as those reliant on flight[12,13]. The metabolic cost of flight is also particularly intensified at high elevations because low air densities require more energy to generate the lift and thrust required for powered flight[14]. Thus, despite the biomechanical potential for much faster dispersal in species that specialize on flight, metabolic constraints should cause flight-dependent species to migrate into the highest elevations more slowly than species that use less metabolically costly modes of locomotion. Nevertheless, no studies have tested whether upslope migration is relatively constrained in flying specialists or in any other taxa with high physiological demands.

To test whether metabolic constraints limit dispersal to higher elevations, we compared rates of upslope migration between insect species that rely completely on flight ('flight-dependent') versus those that can use other, less energetically costly, modes of locomotion ('flight-independent')[15]. Insects are ideal for testing this metabolic constraints hypothesis because insect flight is powered exclusively by aerobic metabolism and its metabolic demands are the highest known in nature[16,17]. We used the BioShifts dataset to compare rates of upslope migration at species' highest elevations (that is, 'leading edge'), mid-elevations (that is, 'centroid') and lowest elevations (that is, 'trailing edge') (Extended Data Table 1)[6]. The results of this analysis provide novel evidence that upslope dispersal to higher elevations is limited in taxa with extreme metabolic demands (Fig. 1).

Across 807 insect species (Extended Data Tables 1 and 2), we found significant differences in the rate of upslope migration between flight-dependent versus flight-independent species at both the leading and trailing edges of species' ranges ($F_{2,656.6} = 9.86$, $P < 0.001$; Fig. 1). At the leading edges of species' ranges, flight-dependent species are migrating slower than those that can use other modes of locomotion ($\beta \pm$ s.e. = -1.93 ± 0.90 m per year; $t_{32.4} = 2.13$, $P = 0.040$; Fig. 1c). Conversely, at the trailing edges of species' ranges, flight-dependent species are moving upslope faster than those species that do not exclusively use flight ($\beta \pm$ s.e. = 3.83 ± 1.47 m per year; $t_{117.2} = 2.61$, $P = 0.010$; Fig. 1a). In the mid-points of species' ranges (centroids), there is high variability in range shifts, and the average dispersal

[1]Department of Integrative Biology, University of Colorado Denver, Denver, CO, USA. [2]School of Biological Sciences, Georgia Institute of Technology, Atlanta, GA, USA. [3]Department of Biology, Washington University in St. Louis, St. Louis, MO, USA. ✉e-mail: michael.p.moore@ucdenver.edu

https://doi.org/10.1038/s41558-023-01794-2

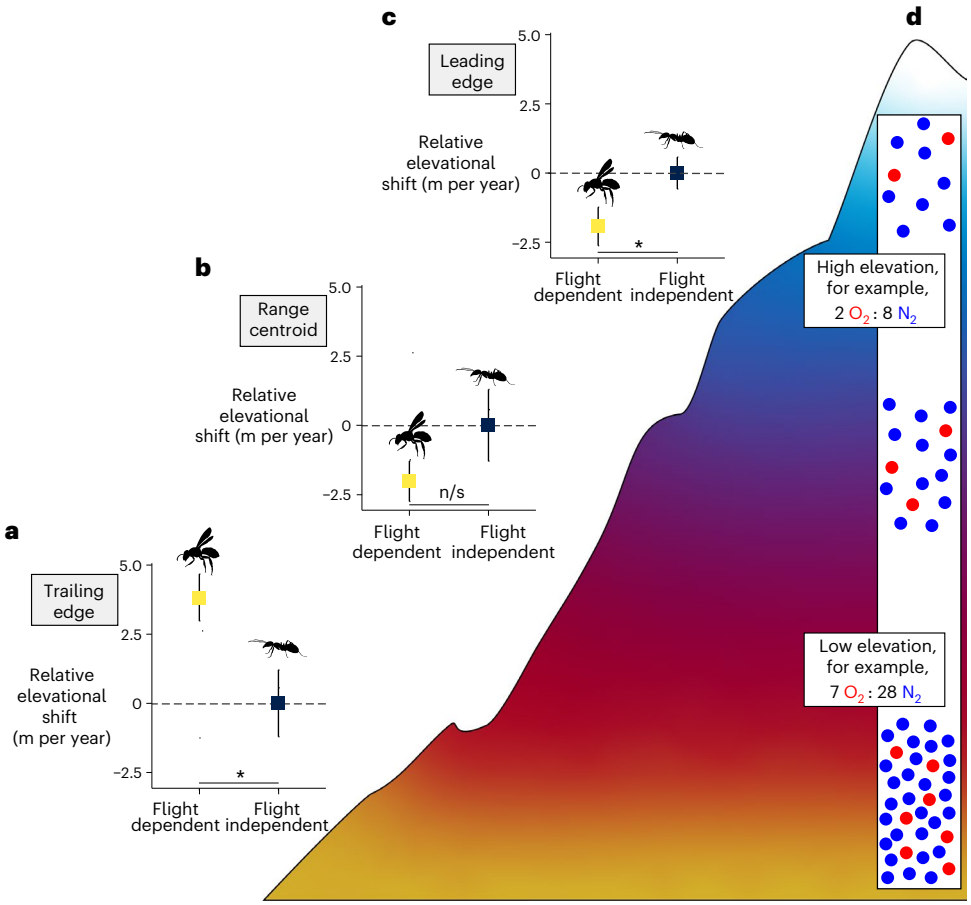

Fig. 1 | Relative rates of upslope migration of flight-dependent insect species compared with species that use less physiologically costly modes of locomotion. a–**c**, Flight-dependent species disperse upslope faster than flight-independent species at lowest elevations (**a**, 'trailing edge'; $n_{\text{flight-dependent}} = 179$ species, $n_{\text{flight-independent}} = 56$ species; $P = 0.010$), show no difference at mid-elevations (**b**, 'range centroid'; $n_{\text{flight-dependent}} = 460$ species, $n_{\text{flight-independent}} = 49$ species; $P = 0.177$) and disperse slower at the highest elevations (**c**, 'leading edge'; $n_{\text{flight-dependent}} = 286$ species, $n_{\text{flight-independent}} = 388$ species; $P = 0.041$). Data are presented as estimated marginal mean ± s.e. from linear mixed-effects models. Asterisks indicate two-sided, post hoc pairwise *t* tests where $P < 0.05$ using the Kenward–Rogers degrees-of-freedom approximation. Silhouettes are from M. Broussard (bee: https://creativecommons.org/licenses/by/3.0/legalcode) and M. Menchetti (ant: https://creativecommons.org/publicdomain/zero/1.0/). **d**, Conceptual diagram of how atmospheric conditions change with increasing elevation.

rates do not differ significantly between the locomotor strategies ($t_{106.7} = -1.36$, $P = 0.177$; Fig. 1b).

Although flight is expected to promote latitudinal and elevational range shifts[18], these results show that the dispersal benefits of flight are lost as the environment becomes more metabolically challenging. At the trailing edges of their geographic ranges, flight-dependent species are migrating upslope 4 m per year faster than species that rely less on flight; a pattern expected as the lowest elevations do not impose the metabolic constraints on flight that are associated with the atmospheric conditions present at higher elevations[14]. However, for every 1,000 m gained above sea level, air pressure declines by ~12 kPa and relative oxygen availability by ~8% (ref. 11). We should therefore expect that flight's metabolic costs will be most restrictive to upslope dispersal at higher elevations. Indeed, flight-dependent species lose their dispersal advantage by the mid-point of their elevational ranges and are at a disadvantage at the leading edge (Fig. 1b). The gradual loss of dispersal advantages along species' elevational ranges is consistent with flight becoming progressively more difficult with increasing elevation rather than impossible only once some absolute threshold is surpassed. In light of these results, there is a need for more research into the barriers on upslope migration due to absolute elevation versus elevational conditions beyond what a species has historically adapted to. Since high-elevation environments present numerous physiological and ecological challenges in addition to the atmospheric conditions, it would also be valuable to investigate how upslope migration is impeded by other barriers facing flight-dependent species, including scarce food, strong winds, extreme cold snaps and intense ultraviolet radiation[7–11]. Nevertheless, the findings of this study are consistent with the prediction that species with high metabolic demands are constrained from migrating upslope in response to climate change[11,12].

For montane species that are metabolically constrained from upslope dispersal, phenotypic plasticity and/or rapid evolution may be necessary to facilitate species persistence[2–4,7]. Unfortunately, it remains unclear whether these alternative responses can rescue taxa from the threat of extinction[2]. For example, increasing upper thermal tolerance limits via acclimation or adaptation could help taxa that are unable to migrate. However, recent syntheses show that such responses are, on average, insufficient to keep pace with contemporary climate change[2,19,20]. Alternatively, natural selection at higher elevations could favour traits that facilitate flight in challenging atmospheric conditions, providing an evolutionary pathway to increased migration success at higher elevations. Nonetheless, this too is an unlikely solution since evolutionary transitions to high-elevation environments are uncommon and often take thousands of generations[21,22]. Thus, while metabolic constraints could prevent many flight-dependent species

from escaping to higher elevations as the planet warms, it is unclear whether other mechanisms can extricate them from these rapidly changing conditions either[23].

If high-elevation environments cannot support immigration from species with physiologically demanding flight, they may also fail to sustain immigration by taxa with other extreme aerobic and metabolic needs. Indeed, a recent synthesis showed that another group of organisms with extremely high metabolic demands, endotherms, is dispersing to higher elevations more slowly than their counterparts with lower metabolic needs, ectotherms[6]. Though that finding has been attributed to endotherms having broader thermal tolerances[6,7], it could alternatively be explained by metabolic constraints[12]. To more fully test the metabolic constraints hypothesis, it would be valuable to examine whether other major differences in metabolism, such as those associated with active versus ambush foraging strategies[24], further shape discrepancies in upslope migration. Additionally, the metabolic constraints hypothesis might apply to a lesser degree for species with extreme metabolic demands during only a subset of essential activities, such as those animals that must produce elaborate vocalizations to coordinate mating[15,24]. An interesting system in which to further study these patterns could be species that exhibit wing polymorphisms—where only a portion of a population's individuals can fly at all[25]—because they could experience constraints on upslope migration that are intermediate to species that depend on flight and those that do not. Ultimately, the animal kingdom exhibits wide variation in aerobic and metabolic demands[23], and this study suggests that those requirements could be an important predictor of upslope migration[11,12].

With substantial population declines occurring for much of the planet's biodiversity[1]—particularly among insects[26,27]—understanding local extinctions and improving conservation strategies require that we detail the factors that make species vulnerable to human impacts[11]. Whereas dispersal is expected to be an important response to rising temperatures[4–7], the present study suggests that some of the putatively best-dispersing taxa are physiologically constrained from migrating to thermally suitable habitats at higher elevations. The large and extremely diverse group of animals that rely solely on flight could therefore be particularly imperilled by climate change at mid and high elevations. Because warm environments further intensify metabolic demands in ectotherms[11,12], any physiological constraints on upslope migration might also be especially acute for the diverse assemblages of flight-dependent insects found in the Tropics[28]. Conservation of flight-dependent species may consequently require more substantial, immediate and widespread human interventions than we have anticipated[27], including, for example, the protection and/or new development of corridors that minimize distances between suitable habitat patches[23]. More generally, as we continue to consider where and how different species will be able to live in the coming decades, this study emphasizes that we should incorporate a fuller scope of species' physiological and ecological requirements into our forecasts[12]. Even if thermally suitable environments are nearby, the capacity for species to disperse and persist in those habitats will be dictated by more than just their thermal preferences.

Online content

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41558-023-01794-2.

References

1. Pörtner, H. O. et al. *Scientific outcome of the IPBES-IPCC co-sponsored workshop on biodiversity and climate change*. (IPBES Secretariat, 2021).
2. Martin, R., da Silva, C. R. B., Moore, M. P. & Diamond, S. E. When will a changing climate outpace adaptive evolution? *Wiley Interdiscip. Rev. Clim.* (in the press).
3. Moore, M. P. et al. Sex-specific ornament evolution is a consistent feature of climatic adaptation across space and time in dragonflies. *Proc. Natl Acad. Sci. USA* **118**, e2101458118 (2021).
4. Parmesan, C. Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.* **37**, 637–669 (2006).
5. 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).
6. Lenoir, J. et al. Species better track climate warming in the oceans than on land. *Nat. Ecol. Evol.* **4**, 1044–1059 (2020).
7. Freeman, B. G., Song, Y., Feeley, K. J. & Zhu, K. Montane species track rising temperatures better in the tropics than in the temperate zone. *Ecol. Lett.* **24**, 1697–1708 (2021).
8. Feeley, K. J., Rehm, E. & Stroud, J. T. There are many barriers to species migrations. *Front. Biogeogr.* **6**, fb_22006 (2014).
9. Mamantov, M. A., Gibson-Reinemer, D. K., Linck, E. B. & Sheldon, K. S. Climate-driven range shifts of montane species vary with elevation. *Glob. Ecol. Biogeogr.* **30**, 784–794 (2021).
10. Rehm, E. M., Olivas, P., Stroud, J. & Feeley, K. J. Losing your edge: climate change and the conservation value of range-edge populations. *Ecol. Evol.* **5**, 4315–4326 (2015).
11. Spence, A. R. & Tingley, M. W. The challenge of novel abiotic conditions for species undergoing climate-induced range shifts. *Ecography* **43**, 1571–1590 (2020).
12. Jacobsen, D. The dilemma of altitudinal shifts: caught between high temperature and low oxygen. *Front. Ecol. Environ.* **18**, 211–218 (2020).
13. Altshuler, D. L. & Dudley, R. Adaptations to life at high elevation: an introduction to the symposium. *Integr. Compar. Biol.* **46**, 3–4 (2006a).
14. Altshuler, D. L. & Dudley, R. The physiology and biomechanics of avian flight at high altitude. *Integr. Compar. Biol.* **46**, 62–71 (2006b).
15. Reinhold, K. Energetically costly behaviour and the evolution of resting metabolic rate in insects. *Funct. Ecol.* **13**, 217–224 (1999).
16. Videler, J. J. *Avian Flight* (Oxford Univ. Press, 2006).
17. Harrison, J. F., Greenlee, K. J. & Verberk, W. C. Functional hypoxia in insects: definition, assessment, and consequences for physiology, ecology, and evolution. *Annu. Rev. Entomol.* **63**, 303–325 (2018).
18. Neate-Clegg, M. H. & Tingley, M. W. Building a mechanistic understanding of climate-driven elevational shifts in birds. *PLOS Clim.* **2**, e0000174 (2023).
19. Radchuk, V. et al. Adaptive responses of animals to climate change are most likely insufficient. *Nat. Commun.* **10**, 3109 (2019).
20. Seebacher, F., White, C. R. & Franklin, C. E. Physiological plasticity increases resilience of ectothermic animals to climate change. *Nat. Clim. Change* **5**, 61–66 (2015).
21. Lack, J. B., Monette, M. J., Johanning, E. J., Sprengelmeyer, Q. D. & Pool, J. E. Decanalization of wing development accompanied the evolution of large wings in high-altitude *Drosophila*. *Proc. Natl Acad. Sci. USA* **113**, 1014–1019 (2016).
22. Moore, M. P. & Khan, F. Relatively large wings facilitate life at higher elevations among Nearctic dragonflies. *J. Anim. Ecol.* **92**, 1613–1621 (2023).
23. Freeman, B. G., Scholer, M. N., Ruiz-Gutierrez, V. & Fitzpatrick, J. W. Climate change causes upslope shifts and mountaintop extirpations in a tropical bird community. *Proc. Natl Acad. Sci. USA* **115**, 11982–11987 (2018).
24. White, C. R. & Kearney, M. R. Determinants of inter-specific variation in basal metabolic rate. *J. Comp. Phys. B* **183**, 1–26 (2013).

25. Zera, A. J. & Denno, R. F. Physiology and ecology of dispersal polymorphism in insects. *Annu. Rev. Entomol.* **42**, 207–230 (1997).
26. Sánchez-Bayo, F. & Wyckhuys, K. A. Worldwide decline of entomofauna: a review of its drivers. *Biol. Conserv.* **232**, 8–27 (2020).
27. Harvey, J. A. et al. International scientists formulate a roadmap for insect conservation and recovery. *Nat. Ecol. Evol.* **4**, 174–176 (2020).
28. Perez, T. M., Stroud, J. T. & Feeley, K. J. Thermal trouble in the tropics. *Science* **351**, 1392–1393 (2016).

Methods

Data compilation

We assembled a dataset on both elevational range shifts and locomotor strategies for 807 insect species. To gather data on species' elevational range shifts, we used the comprehensive BioShifts dataset[6,29], which is a compilation of latitudinal and elevational range shifts at the trailing edge, centroid and leading edge of species' ranges. It contains elevational range shifts for >1,700 animal species from all over the planet. We then used publicly available species' descriptions to classify each species in the dataset either as being nearly or completely reliant on flight ('flight-dependent species') or as having other options for locomotion ('flight-independent species')[15]. We recognize that all or some (that is, wing polymorphisms) individuals within a species could be capable of powered flight in the 'flight-independent' group, but we use this terminology to align with earlier analyses (see, for example, ref. 15). When there was no species' description available, we used the classifications of congeneric species. All records for locomotor strategy were checked by two people.

Statistical analysis

We compared patterns of upslope migration between flight-dependent and flight-independent species with linear mixed-effects models[30]. We used the rate of elevational range shift for each species as the response variable, whereby large positive values indicate fast upslope migration and large negative values indicate fast downslope migration. We included each species' locomotor strategy as a fixed effect. To test whether range shifts differ at species' highest versus lowest elevations, we also modelled a fixed effect of range position (trailing edge, centroid and leading edge) as well as the interaction between range position and locomotor strategy. Finally, to control for the possibility that the mean rate of range shifts depends on the initial year in which the species were monitored, we also included the starting year as a covariate. Following ref. 6, we included a species' genus and family as random effects to control for shared evolutionary history. Because each species could have an estimate of a range shift for each position, we included a random effect for species to account for the repeated measures. We tested for significance using F-tests with the Kenward–Roger denominator degrees-of-freedom approximation[31]. Since the hypotheses we are testing concern the rates of upslope migration of flight-dependent species relative to flight-independent species at each range position, we defined contrasts to specifically test the difference in migration rate between locomotor strategies at the trailing edge, at the centroid and at the leading edge of species' ranges (see Extended Data Tables 1 and 2 for sample sizes). We report all effect sizes as the regression-estimated difference ± s.e. in upslope migration rate between flight-dependent species relative to flight-independent species. If metabolic constraints limit dispersal into the highest elevations, then flight-dependent species should migrate upslope slower than flight-independent species at the leading edge of species' ranges.

As the BioShifts dataset is a compilation of range shift measurements from many different types of studies, the original analysis presented by Lenoir and colleagues[6] attempted to control for heterogeneity in the estimates by including several additional random effects in their analysis. We therefore conducted analyses with the same suite of random effects as they did in their analyses, but the results were always the same. We report the results of these supplemental analyses in Extended Data Tables 3–6.

Data availability

Data underlying this study can be accessed through the Dryad Digital Repository at https://doi.org/10.5061/dryad.kh18932bs (ref. 32).

Code availability

Code underlying this can be accessed through the Dryad Digital Repository at https://doi.org/10.5061/dryad.kh18932bs (ref. 32).

References

29. Comte L., et al. BioShifts: a global geodatabase of climate-induced species redistribution over land and sea. *Figshare* https://doi.org/10.6084/m9.figshare.7413365 (2020).
30. Bates, D., Maechler, M., Bolker, B. & Walker, S. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48 (2015).
31. Kuznetsova, A., Brockhoff, P. B. & Christensen, R. H. B. lmerTest: tests in linear mixed effects models. *J. Stat. Softw.* **82**, 1–26 (2017).
32. Moore, M. P. Data from: upslope migration is slower in species with high physiological demands. *Dryad Digital Repository* https://doi.org/10.5061/dryad.kh18932bs (2023).

Acknowledgements

Support was generously provided by the University of Colorado Denver (to M.P.M. and J.S.) and Washington University in St. Louis and the Georgia Institute of Technology (to J.T.S.). Conversations with J. de Mayo, J. Grady and A. Lenard and input from three reviewers improved this study.

Author contributions

M.P.M. designed the study. J.S. and M.P.M. collected the data. M.P.M. and J.T.S. analysed the data. M.P.M. and J.T.S. wrote the paper.

Competing interests

The authors declare no competing interests.

Additional information

Extended data The online version contains supplementary material is available for this paper at https://doi.org/10.1038/s41558-023-01794-2.

Correspondence and requests for materials should be addressed to Michael P. Moore.

Peer review information *Nature Climate Change* thanks Dean Jacobsen, Lourenço Martins and the other, anonymous, reviewer(s) for their contribution to the peer review of this work.

 https://doi.org/10.1038/s41558-023-01794-2

Extended Data Table 1 | Number of estimates of upslope migration (meters per year) for flying and non-flying species

Strategy	Leading Edge	Centroid	Trailing Edge
Flying Species	286	460	179
Non-Flying Species	388	49	56

Numbers of estimates for the rate of upslope migration (meters per year) between flying and non-flying species at the leading edge, centroid, and trailing edge of species' elevation ranges.

https://doi.org/10.1038/s41558-023-01794-2

Extended Data Table 2 | Numbers of estimates of upslope migration (meters per year) by insect family

Family	Centroid	Leading Edge	Trailing Edge
Andrenidae	0	4	0
Anobiidae	0	1	0
Anostostomatidae	0	2	2
Anthribidae	0	1	0
Aphodiidae	7	7	7
Apidae	235	22	17
Brachyceridae	0	1	0
Brentidae	0	3	0
Buprestidae	0	2	0
Byrrhidae	0	2	0
Byturidae	0	1	0
Cantharidae	0	12	0
Carabidae	0	50	5
Cerambycidae	0	16	0
Cerylonidae	0	3	0
Chrysididae	0	2	0
Chrysomelidae	0	14	0
Ciidae	0	6	0
Cleridae	0	2	0
Clusiidae	1	0	0
Coccinellidae	0	7	0
Crabronidae	0	4	0
Cryptophagidae	0	5	0
Curculionidae	0	40	0
Diprionidae	0	1	0
Dytiscidae	0	4	0
Elateridae	0	13	0
Erotylidae	0	1	0
Formicidae	0	6	0
Geometridae	124	132	134
Geometridqe	2	2	2
Geotrupidae	3	5	3
Hesperiidae	0	1	1
Hydrophilidae	0	3	0
Latridiidae	0	3	0
Leiodidae	0	7	0
Lucanidae	0	1	0
Lycaenidae	0	3	2
Lycidae	0	2	0
Lymexylidae	0	1	0
Melandryidae	0	1	0
Meloidae	0	1	0
Melolonthidae	0	1	0
Melyridae	0	4	0
Monotomidae	0	2	0
Mordellidae	0	1	0
Nitidulidae	0	11	0
Notodontidae	0	1	0
Nymphalidae	67	21	19
Oecophoridae	1	0	0
Oedemeridae	0	1	0
Pamphiliidae	0	1	0
Papilionidae	5	1	1
Perlidae	2	2	0
Pieridae	23	1	1
Pompilidae	0	1	0
Ptiliidae	0	3	0
Ptinidae	0	1	0
Pyrochroidae	0	1	0
Scarabaeidae	39	48	39
Scirtidae	0	3	0
Scraptiidae	0	2	0
Silphidae	0	4	0
Siricidae	0	1	0
Sphaeritidae	0	1	0
Staphylinidae	0	78	0
Syrphidae	0	50	0
Tenebrionidae	0	2	0
Tenthredinidae	0	30	0
Trogossitidae	0	2	0
Vespidae	0	6	0
Zygaenidae	0	0	2

Numbers of estimates for the rate of upslope migration (meters per year) by family at the leading edge, centroid, and trailing edge of species' elevation ranges.

 https://doi.org/10.1038/s41558-023-01794-2

Extended Data Table 3 | Comparison of elevational range shifts between flying specialists and locomotor generalists when using full set of possible random effects

Range Position	Estimate ± SE	t	P
Leading Edge	-1.93 ± 0.95	-2.037	0.050
Centroid	-2.02 ±1.50	-1.345	0.182
Trailing	3.83 ± 1.53	2.508	0.014

Comparison of range shifts between flying specialists and locomotor generalists at the trailing edge, centroid, and leading edge of species' ranges using as many of the random effects as possible from the Lenoir et al. (ref. 6) analysis. In addition to random intercepts for species, genus, and family, this analysis included random intercepts for the following: the quality of the sampling; the sampling strategy; the grain of the sampling; and whether the sampling was conducted using changes in presence/absence or changes in abundance. Sample sizes are as in Table S1, and all values are from two-sided post-hoc tests from the linear-mixed effects models with the Kenward-Rogers denominator degrees of freedom approximation.

 https://doi.org/10.1038/s41558-023-01794-2

Extended Data Table 4 | Comparison of elevational range shifts between flying specialists and locomotor generalists using random effects where each level had at least 6 replicates

Range Position	Estimate ± SE	t	P
Leading Edge	-1.93 ± 0.93	-2.068	0.047
Centroid	-2.02 ± 1.50	-1.346	0.181
Trailing	3.83 ± - 1.52	2.513	0.013

Comparison of range shifts between flying specialists and locomotor generalists at the trailing edge, centroid, and leading edge of species' ranges using the random effects from the Lenoir et al. (ref. 6) analysis for which there was sufficient replication among levels (n>6) within our subsetted dataset of just insects species. This analysis therefore included random intercepts for the quality of sampling and whether the sampling was conducted using changes in presence/absence or changes in abundance. Sample sizes are as in Table S1, and all values are from two-sided post-hoc tests from the linear-mixed effects models with the Kenward-Rogers denominator degrees of freedom approximation.

https://doi.org/10.1038/s41558-023-01794-2

Extended Data Table 5 | Comparison of elevational range shifts between flying specialists and locomotor generalists using random effects that account for sampling methodology

Range Position	Estimate ± SE	t	P
Leading Edge	-1.93 ± 0.91	-2.126	0.041
Centroid	-2.02 ± 1.50	-1.352	0.179
Trailing	3.83 ± 1.47	2.601	0.011

Comparison of range shifts between flying specialists and locomotor generalists at the trailing edge, centroid, and leading edge of species' ranges using a random intercept for whether the sampling was conducted using changes in presence/absence or changes in abundance. Sample sizes are as in Table S1, and all values are from two-sided post-hoc tests from the linear-mixed effects models with the Kenward-Rogers denominator degrees of freedom approximation.

https://doi.org/10.1038/s41558-023-01794-2

Extended Data Table 6 | Comparison of elevational range shifts between flying specialists and locomotor generalists using random effects for the quality of sampling

Range Position	Estimate ± SE	t	P
Leading Edge	-1.93 ± 0.93	-2.074	0.046
Centroid	-2.02 ± 1.49	1.353	0.179
Trailing	3.83 ± 1.52	2.526	0.013

Comparison of range shifts between flying specialists and locomotor generalists at the trailing edge, centroid, and leading edge of species' ranges using a random intercept for the quality of sampling. Sample sizes are as in Table S1, and all values are from two-sided post-hoc tests from the linear-mixed effects models with the Kenward-Rogers denominator degrees of freedom approximation.