



Elevational homogenization of mountain parasitoids across six decades

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Elevational gradients are characterized by strong environmental changes within small geographical distances, providing important insights on the response of biological communities to climate change. Mountain biodiversity is particularly sensitive to climate change, given the limited capacity to colonize new areas and the competition from upshifting lowland species. Knowledge on the impact of climate change on mountain insect communities is patchy, but elevation is known to influence parasitic interactions which control insect communities and functions within ecosystems. We analyzed a European dataset of bristle flies, a parasitoid group which regulates insect herbivory in both managed and natural ecosystems. Our dataset spans six decades and multiple elevational bands, and we found marked elevational homogenization in the host specialization of bristle fly species through time. The proportion of specialized parasitoids has increased by ca. 70% at low elevations, from 17 to 29%, and has decreased by ca. 20% at high elevations, from 48 to 37%. As a result, the strong elevational gradient in bristle fly specialization observed in the 1960s has become much flatter over time. As climate warming is predicted to accelerate, the disappearance of specialized parasitoids from high elevations might become even faster. This parasitoid homogenization can reshape the ecological function of mountain insect communities, increasing the risk of herbivory outbreak at high elevations. Our results add to the mounting evidence that symbiotic species might be especially at risk from climate change: Monitoring the effects of these changes is urgently needed to define effective conservation strategies for mountain biodiversity.

climate change | functional homogenization | insect decline | mountain biodiversity | parasitoid

Mountains face a dual reality when it comes to climate change: They can act as climatic refugia, with lower climate velocity than lowlands (1), but they can also be climatic traps for mountain-top species with limited ability to migrate to new areas, much like islands (2). Species living at higher elevations often have specialized ecological niches which make them particularly sensitive to rapid environmental change (3); they also suffer competition from lowland generalist species that show upward shift following climatic alteration. For example, in an analysis of small mammal communities in the Yosemite National Park (USA), Moritz and colleagues found that *r*-strategist lowland species (i.e., short-lived and highly fecund) were more likely to expand their range upward compared to their long-lived, less fecund, counterparts (4). These upward range shifts of lowland species were associated with range contractions and decline of specialized high-elevation species. Evidence of changes in the composition of mountain insect communities (3, 5, 6) is less well documented compared to vertebrates (4, 7–9), reflecting a widespread bias in conservation literature (10–12). However, recent work suggests that global insect decline might be as serious, if not more severe, than that of vertebrate species (13), including in mountain areas (3).

Maunsell and colleagues (14) found that elevation strongly influenced both the strength and existence of parasitic interactions among insects, with a key role of climate change in altering them. As elevation increases, the period during which hosts are active becomes shorter, generating a turnover in host availability and potentially leading to parasitic specialization. Likewise, Morris and colleagues found higher level of specialization at higher elevation in a subtropical host–parasitoid network (15). This was driven by climate and environmental factors but was also related to the reduced number of host species available at higher elevation (i.e., reduced host diversity driving specialization). These results add to the mounting evidence that symbiotic species might be especially sensitive to climate change (16, 17). Predator and parasitoid insects—those that have parasitic larvae and free-living adults—are crucial in regulating population dynamics of their prey/hosts in both natural and managed environments, but climate change can alter these dynamics (18). Parasitoid insects, such as bristle flies (Diptera: Tachinidae) and several wasps (Hymenoptera), play an especially important role in

Significance

Mountain species are highly sensitive to climate change, but knowledge of climate impact on insect communities is limited. We analyzed a six-decade dataset of European bristle flies, a parasitoid group which regulates insect herbivory within both managed and natural ecosystems. We found that the proportion of specialized parasitoids has increased by 70% at low elevations and decreased by 20% at high elevations. This resulted in a progressive homogenization of bristle fly diet across elevational bands. This homogenization can reshape the ecological function of mountain insect communities, increasing the risk of herbivory outbreak at high elevations. As global warming is predicted to accelerate, the disappearance of specialized parasitoids from high elevations might become faster.

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mountain ecosystems (19, 20), controlling the density of phytophagous insects and their impact on natural vegetation. Moreover, adult bristle flies feed on nectar, like other parasitoid dipterans, and play an important pollination role. This role is especially key in temperate mountain ecosystems, where flies can functionally replace bees as ecosystem pollinators (21). Yet, parasitoids are often the first ecosystem component to respond to global environmental changes (22, 23).

Climate change can affect parasitoids directly, i.e., by alteration of their phenology and distribution, and indirectly by influencing the phenology and distribution of their hosts (24). Any shifts in the phenology or distribution of host species, in response to climate variation, may result in a temporal/spatial lag that reduces the ability of parasitoids to control host populations. This effect can be further exacerbated in specialized parasitoids, where the fragmentation of potential hosts distribution can hamper their range expansion (24). The ecological impact triggered by the loss of a parasitoid species depends on the degree of ecological redundancy of the species within the ecosystem. Often, the role of specialized parasitoids is unlikely to be fully replaced by other species in the short term, as specialized parasitoids are much more effective at exploiting their target host compared to generic ones. This might be the case for bristle flies that evolved specialized host-location capacity to attack caterpillars with specific plant preferences, as well as bristle flies that evolved specific physiological resistance to toxins produced by aposematic caterpillars (25). The loss of such specialized parasitoids might generate functional disruptions that lead to host outbreaks. This is a symptom of functional homogenization, where specialist species are replaced by generalist ones due to global change (26), with a consequent loss of certain ecosystem functions. But is this especially the case in mountain areas?

Here, we analyze an exceptional dataset of parasitoid bristle flies consisting of species occurrence from several parts of Europe, spanning six decades (since 1960) and multiple elevational bands (sea level to mountain top at 2,900 m asl). Bristle fly species can feed on a variety of hosts—caterpillars, beetles, bugs, etc.—and show varying degrees of host specialization: from hyperspecialists that feed on a single host species to complete generalists that can use hosts from many different families (20). We investigated the temporal trend in the probability of sampling bristle flies with a specialized diet (i.e., “oligophagous” species) across multiple elevations to estimate whether the elevational gradient in parasitoid specialization has changed over time as a symptom of functional homogenization. Specialized niches are typically favored in stable environments while heterogeneous conditions generated by environmental change often

favor the persistence (or arrival) of generalists. Additionally, while short-term environmental variation generally favors species coexistence, long-term variation—such as that driven by climate change—promotes competitive exclusion (27). Here, we hypothesized that the elevational gradient in specialized parasitoids has reduced over time, as high-elevation specialists are highly sensitive to climate change (especially global warming) and suffer competition from lowland generalists (i.e., “polyphagous” species) which can move upward under climate change.

Results

While sampling effort in our data was not homogeneous through space and time, multiple elevational bands and multiple areas were sampled in each decade (*SI Appendix, Figs. S1 and S2*). We run a generalized additive model (GAM), with binomial family, accounting for spatial autocorrelation, the phylogenetic position of species, and several potential sources of sampling bias (*Materials and Methods and SI Appendix, Appendix S1*). The model predicted the probability of sampling specialist species and showed significant influence of both year and elevation of sampling (*SI Appendix, Table S1*). We found marked differences in the temporal trend of specialized feeders across elevational bands (Fig. 1). At low elevation, with 250 m asl as a reference, the proportion of specialized feeders’ occurrences showed an increase through time, from 17.4% in 1960 (se = 3.0%) to 29.2% in 2019 (se = 6.2%), i.e., a ca. 70% relative increase over the course of six decades. At higher elevation instead, we found increasingly steep decline in the proportion of specialized feeders’ occurrences. At high elevation, with 1,750 m asl as a reference, the proportion of specialized species has dropped from 47.7% (se = 8.8%) to 37.2% (se = 8.6%), i.e., a ca. 20% relative decrease.

While the proportion of specialized feeders followed a strong elevational gradient in the 1960s, i.e., higher proportions at higher elevation, the trend became much flatter in 2019 (Fig. 2). During the same period, locations in our study region faced a steady increase in temperature, with an average global warming of 0.034 °C/y (se = 0.0005 °C/y; *SI Appendix, Fig. S3*). This result supports our hypothesis of a progressive, climate-driven, homogenization of parasitoid diets across elevational bands. To test whether temporal bias in sampling effort affected our results, we also repeated our analysis on a high-quality subset of our dataset (covering the locations with the best sampling effort over time). Our test confirmed the trends reported in the original model (*SI Appendix, Figs. S4 and S5*). We further tested whether a few common species were driving our results, excluding species with exceptional representation in our

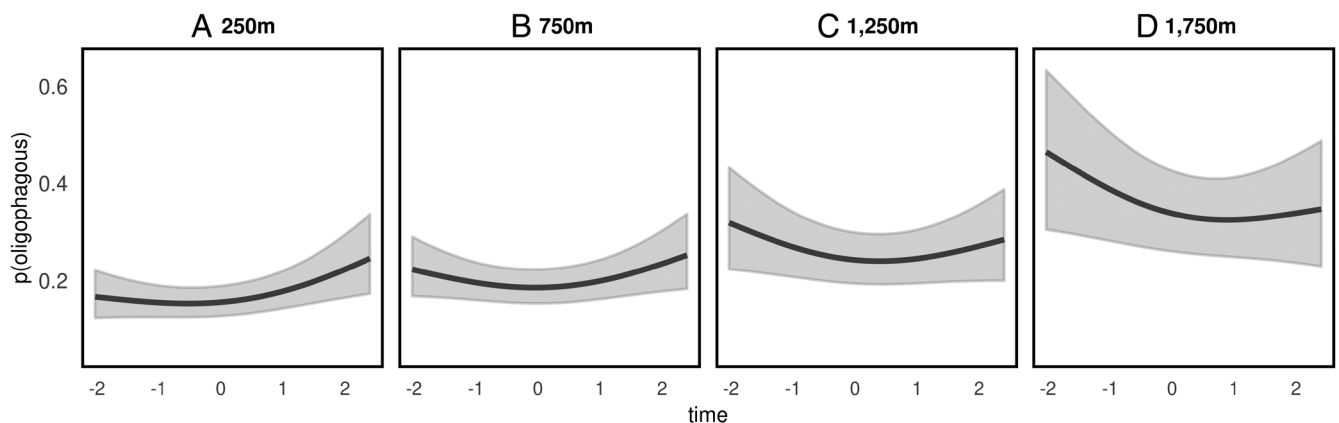


Fig. 1. Predicted temporal trend in the proportion of specialized bristle flies (i.e., oligophagous species) sampled at different representative elevational bands. Each plot represents a 60-y trend in the probability of sampling specialized species at a different elevation (A–D, as indicated on top of the plots). Values on the x axis (i.e., years between 1960 and 2019) have been rescaled for analysis.

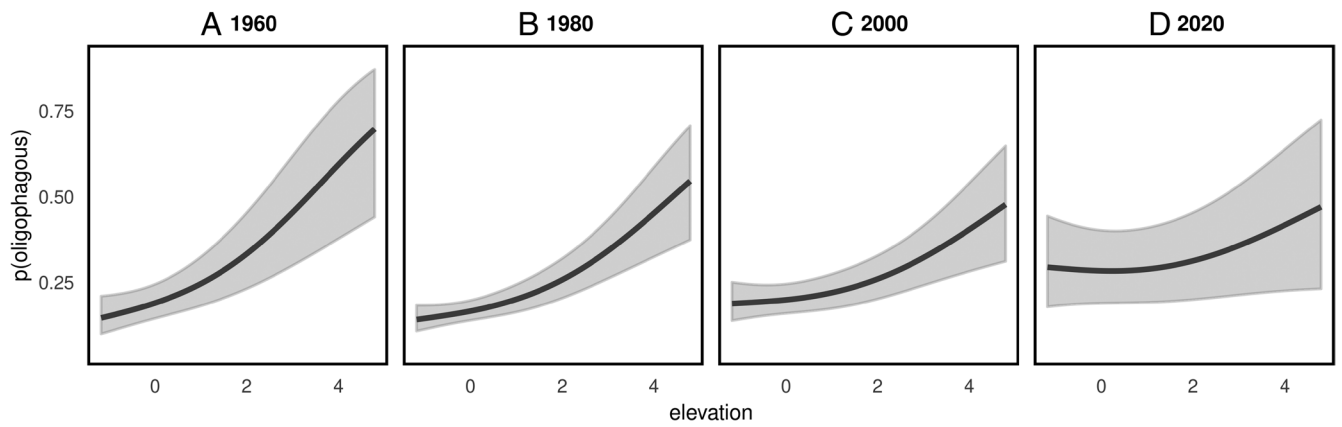


Fig. 2. Predicted elevational trend in the proportion of specialized bristle flies (i.e., oligophagous species) through time. Each plot represents a >2,000 m elevational trend in the probability of sampling specialized species in a given year (A–D, as indicated on top of the plots). Values on the x axis (i.e., meters asl) have been rescaled for analysis.

dataset; once again, the test confirmed the trends reported in the original model (*SI Appendix, Figs. S6 and S7*).

The homogenization pattern we found depended on multiple co-occurring dynamics (Fig. 3), which we investigated by looking at single-species trends. We estimated elevational trends for each species as the linear relationship between elevation vs. year of sampling; the slopes of these relationships represent the average elevational shift for each species in terms of meters/year (*SI Appendix, Fig. S8*). At low elevations, generalist species were twice as fast (median \pm se: 5.2 ± 0.98 m/y) in their elevational upshift compared to specialist species (2.4 ± 1 m/y). One such example is *Pales pavida*, a frequently sampled generalist feeder able to parasitize over 20 different lepidopteran families (Fig. 3A); this species was found only below 1,000 m asl until

the mid-1970s but has become common at almost every elevational band since year 2000. At high elevations instead, both groups showed rapid, and similar, elevational upshift through time (generalists: 7.7 ± 1.27 m/y; specialists: 7.9 ± 1.15 m/y). However, while highland generalist species were typically able to maintain wide elevational range through time, many highland specialists—such as *Nowickia atripalpis* (Fig. 3D), which feeds on a single family of lappet moths (*Lasiocampidae*)—have shrunk their elevational range toward higher elevation. These values of elevational shift are broadly in line with the average warming of 0.034 °C/y observed across our sampling locations, equivalent to a 3.4 m/y elevational shift in climatic conditions (if assuming a change in temperature of ca. 1 °C for every 100 m of elevation).

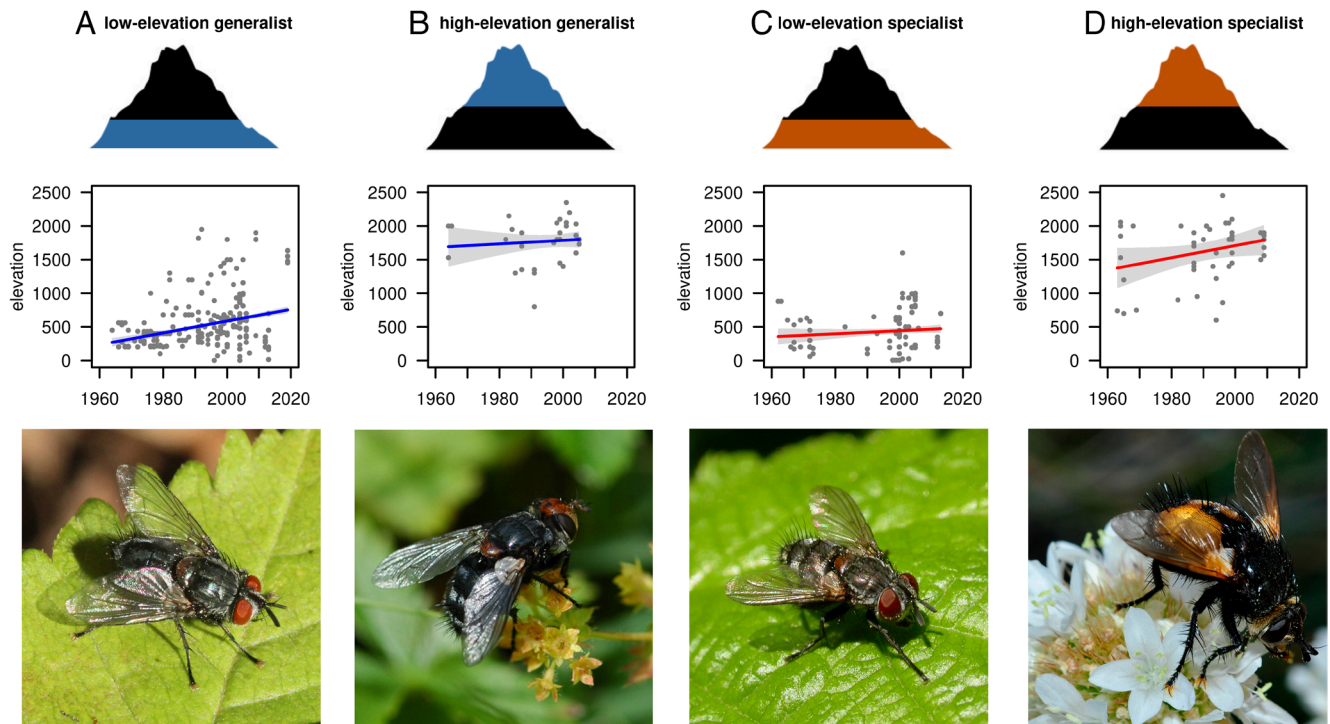


Fig. 3. Temporal trend in the sampling elevation of four commonly sampled bristle fly species. (A) *Pales pavida*, a low-elevation generalist feeder (polyphagous) which showed rapid elevational shift through time (Photo credits: Piluca Álvarez Fidalgo); (B) *Onychogonia flaviceps*, a high-elevation generalist feeder which showed a stable elevational range (Photo credits: Cor Zonneveld); (C) *Carcelia falenaria*, a low-elevation specialized feeder (oligophagous) which showed slow elevational shift (Photo credits: Pierfilippo Cerretti); (D) *Nowickia atripalpis*, a high-elevation specialized feeder which showed elevational contraction toward high elevations (Photo credits: Francisco Rodríguez Luque). Points represent actual sampled occurrences, while lines represent linear trends. *SI Appendix, Fig. S8* shows the slope of the temporal trend for all species with sufficient sampling coverage. Mountain silhouette from Vecteezy.com.

Discussion

Climate change is altering the composition of biological communities worldwide, and its impact on insects is now widespread, including alteration of their phenology (28), diversity (29), biomass (30), and migration (31). This impact might be disproportionately affecting certain groups of insects, such as parasitoids, which are in turn dependent on the distribution, abundance, and phenology of their host species. For example, Corcos and colleagues (6) found that species richness and evenness of bristle flies decreased with elevation, as mean temperature was positively associated with both variables. This was probably due to high temperatures enhancing plant productivity, hence host availability, and extending parasitoid foraging time. Here, we found a homogenization in the elevational gradient of parasitoids specialization as a result of climate change.

Our results showed a reshuffling of host specialization in bristle flies along elevational bands, with specialized species becoming less common at high elevations. This pattern was driven by several concurrent dynamics, the main one being the ability of lowland generalist species to quickly colonize higher elevations. Many generalist feeders have rapidly expanded their ranges to higher elevations, suggesting that they are either effectively tracking host range shifts or efficiently exploiting new hosts in newly colonized elevational belts. The majority of generalist species showed elevational shifts over time, reflecting a pattern already observed in groups such as butterflies (3) and small mammals (4). These species may be more tolerant to changes in rainfall and temperature with respect to their herbivore hosts and their feeding plants, but their flexible reproductive and developmental strategies (25, 32) could make them effective at exploiting new hosts as local insect communities change. Lowland specialized feeders instead showed slow upward shift in elevation over time, showing more limited ability at colonizing new elevational belts compared to generalists. While rapid upward shifts characterized both high-elevation specialists and generalists, the former have in some cases disappeared from lower elevations thus making their elevational ranges narrower (e.g., *Nowickia atripalpis*, showed in our example Fig. 3D). These specialists are likely to follow changes in host distribution and should be considered particularly vulnerable to climate change.

Studies of ant communities showed that only a few species are able to survive the harsh climatic conditions of high elevations (5, 33). This pattern may, in principle, apply also to parasitoid insects since lower temperatures at higher elevations may reduce the temporal window during which individuals are active, thereby influencing their efficiency in locating suitable hosts (14). However, climate change can also affect the composition of parasitoid communities indirectly, by altering the spatiotemporal distribution of their hosts. For example, Stireman and colleagues (34) observed a relationship between precipitation variability and parasitism and attributed this relationship to the ability of parasitoid populations to survive on caterpillar populations of varying density. They postulated that highly specialized parasitoids should be more sensitive than generalists to variation in host emergence time or developmental rate, as they may miss narrow windows of vulnerability of their particular hosts. In contrast, generalist parasitoids are more resilient as they exploit a variety of hosts that might have different phenological response to climate change, making them less susceptible to asynchronies associated with climatic change. We found a strong elevational gradient in bristle fly diet specialization in the past and a deterioration of such gradient in the present, with little elevational difference in the proportion of specialized feeders between lowlands

and mountain tops in present days. Our results are compatible with both effects described above, and further research on host species elevational trends is required to disentangle them.

Climate change is widely known to alter the distribution of species by modifying the environmental conditions necessary to their persistence (35, 36), and mountain taxa in particular are undergoing rapid elevational shift to track climate-driven environmental change (4, 37). These uphill movements however depend on species ecology and dispersal capacity (38–40) and can be associated to other adaptation strategies such as shifts in aspects, as complex topography regulates local climatic conditions (41). We found average uphill trends of 2.4 to 7.9 m/y for our study species, depending on the group considered (specialist vs. generalists, lowland vs. highland), which is broadly in line with the average warming observed across our sampling locations. Our results are thus consistent with a general pattern of climate-induced uphill shift in species distribution. Moreover, we found generalist lowland species being substantially faster than specialist lowland species at moving uphill, again confirming patterns already observed in other groups (4). Our results demonstrate the multidimensional impact of climate change, which goes beyond species redistribution, affecting species interactions and ecosystem functions.

While the probability of sampling specialized species at high elevations has decreased over time, such trend seems to be mainly due to a dilution effect, with generalist parasitoids becoming dominant. This may result in higher competition and generate extinction debts: the current diversity in high-elevation parasitoid species may be higher than that expected at ecological equilibrium, if specialized species will go extinct from increased competition. The dual ecology of bristle flies (endoparasitic larvae, nectar-feeding adults) means different species can develop on different host species, without entering direct competition, but then potentially face interspecific competition for nectar as adults. The arrival of generalist bristle flies at high elevations may subject local specialist species to higher competitive pressures during their adult stages. This in turn might affect the ability of specialist species larvae to control the population of certain hosts (herbivore insects), which are either not attacked by generalist species or less susceptible to them (25). The role of interspecific competition in altering species response to climate change has been widely discussed (40) and might explain our results on parasitoid homogenization.

In various host–parasitoid systems, bristle flies have been shown to play an essential role in regulating their hosts' populations, limiting caterpillar outbreaks and thus mitigating defoliation events. Rearing programmes of Lepidoptera and other phytophagous insects conducted in temperate and tropical regions have shown that bristle flies parasitism rates average 7 to 15% among host taxa (with peaks above 50% for particular host species), often exceeding parasitism rates for all parasitoid wasps combined (34, 42). The loss of such specialized parasitoids can be especially problematic for ecosystems sensitive to climate change, if there are no other mechanisms to control the density of herbivore insects, leading to a risk of herbivory outbreaks (43). Functional homogenization, measured as the proportion of specialized species in a community, is considered to be an important indicator of the impact of global change on biodiversity (26). We found increased dietary homogenization of parasitoid insects along elevational gradients, as an effect of upshifting generalist species at the expense of specialist ones. Climate warming is predicted to increase mean annual temperatures and exacerbate weather variability despite international commitments (44), and it is possible that the disappearance of specialized parasitoids from higher elevation will be even faster. These changes in community composition can affect

key ecological dynamics, triggering cascading effects such as outbreaks of host species, negative effects on primary producers, and ecosystem instability (14, 45, 46).

Biodiversity conservation efforts are being scaled up following the recently approved Kunming-Montreal Global Biodiversity Framework (47), yet similar efforts by the Convention on Biological Diversity have not achieved the desired outcome in the past (48–50). Global biodiversity monitoring has failed to fully represent the complex nature of the global biodiversity crisis. Much of the research has focused on species-level impact, typically vertebrates (10–12); instead, ecosystem-wide impacts have received less attention, despite potentially having more widespread consequences (51). Our results show a progressive niche homogenization in a dominant group of mountain parasitoids, with potentially dramatic ecosystem-wide consequences which are yet to be fully understood. Monitoring the effects of these changes is urgently needed to implement informed and effective conservation strategies for mountain ecosystems.

Materials and Methods

Data Collection. We focused our analysis on bristle flies (Diptera: Tachinidae), a parasitoid family of flies with widespread distribution both geographically and elevationally. Bristle flies are a recently evolved group of endoparasitoids, distributed worldwide in terrestrial environments, and capable of feeding on a variety of insects and, to a lesser extent, other arthropods such as centipedes and scorpions (52–54). Less than half of described species have known hosts (55) but, of those known, most attack larval stages of holometabolous insects, especially Lepidoptera and Coleoptera (see ref. 56 for an account of the Palearctic fauna). Although traditionally considered to be polyphagous, evidence is mounting that tachinids are often highly host-specific (20, 57).

In this study, we used a dataset of 60,978 tachinid occurrence records for 782 species from Central and Southern Europe, collected between years 1845 and 2022 (Dataset S1). The dataset was obtained by combining observations based on specimens from museums and private collections; all specimens were identified to species level and records were certified by PC and HPT. Each species was attributed a diet breadth category of either “oligophagous” or “polyphagous,” based on host preferences reported in Tschorsnig (58). Oligophagous were defined as those specialized species feeding on phylogenetically related hosts, belonging to one or two family ranked clades; polyphagous were defined as those generalist species feeding on a wide range of host species, belonging to two or more family ranked clades.

The relative sampling effort across different diet categories remained constant through time; hence, changes in community composition are expected to reflect genuine changes in the probability of the presence of oligophagous and polyphagous species across time and elevation. However, we recognized several sources of bias in our dataset, which we have accounted for in our analysis (Data Analysis).

Data Analysis. We filtered the occurrence data points to remove those without a defined elevational value or precise coordinate locations and those referring to species of unknown dietary preferences. Additionally, given the temporal sparseness of our data before 1960 and after 2019, we only retained records collected between those years (SI Appendix, Fig. S1 and Appendix S1). The filtered dataset consisted of 44,918 occurrence points. Each record in the dataset included species name, phylogenetically defined tribe, elevation, geographic coordinates, name of the location, year of collection, and species diet classification as either “oligophagous” or “polyphagous.” The classification of species into tribes followed past work (53, 59).

We followed the work of Isaac et al. (60) and Boyd et al. (61) in explicitly identifying spatial and temporal bias in our dataset. As our work is aimed to the identification of trends in diet specialization across time and elevation, we did not employ species-specific models but rather a global model with a binary response variable, represented as the presence “1” or absence “0” of specialized diet in a record (i.e., the sampling of an oligophagous species). We examined potential sources of bias in our dataset using the ROBITT tool (61) (SI Appendix, Appendix S1). In particular, we identified a bias in the sampling effort of our dataset through space and through time. To minimize the effects of these biases, we added three

model components designed to address variation in sampling effort (60). First, we ran a location-based filter on our data, by only retaining locations with at least ten occurrence points sampled over at least 15 y (i.e., locations sampled over at least one-quarter of the study period); this resulted in 10,858 records being retained for 418 species. Second, we included a random effect for location identity; both these two components are intended to reduce the effect of uneven spatial coverage of our sampling over time. Third, we added a variable representing overall sampling completeness in each locality to control for uneven sampling effort (see below). Most of the sampling over the six decades was carried out during the months of adult activity for tachinid species, which in Europe is roughly March to November. Also, we did not account for the different detection ability among experts because this does not alter the probability of identifying a specialist vs. generalist species. Our final model, accounting for spatial and temporal bias, was similar to the “ReportingRate” model with additional bias components control reported in Isaac et al. (60), which had good performance under scenarios of temporal change in the number of visits per site (which is similar to our data).

We ran a generalized additive model (GAM) with a binomial family to predict the probability of occurrence records to refer to oligophagous species. The model included smoothed effects of the elevation and year of collection and their parametric interaction. Both variables were rescaled before analysis. To reduce possible overfitting and limit statistical relationships to biologically meaningful responses, we limited the smooth parameter $k = 3$, approximately corresponding to quadratic relationships. To control for varying sampling effort across localities, we included a measure of sample completeness (62) for “incidence data” in the parametrization case of $q = 0$ (i.e., without data on populations abundance). In this case, we approximated sample completeness as the ratio between number of observed species in each location vs. the species diversity estimated with a Chao2 approach. To control for the effect of spatial autocorrelation in sampling localities, we used a trend surface approach (63) including a tensor product smooth of easting and northing. To control for the effects of taxonomy, we added a random effect for phylogenetically defined tribes. To control for the effects of uneven sampling, we added a random effect for location identity. Based on this model, we visualized the relationship between the probability of collecting oligophagous records over time at four representative elevational bands (250 m, 750 m, 1,250 m, and 1,750 m asl) and in two representative years (1960 and 2019).

As our analysis of bias highlighted a decreasing trend in the latitude of sampled location over time (SI Appendix, Appendix S1), we ran a sensitivity test to assess whether our results were a true representation of temporal trend across elevational bands rather than an artifact of biased sampling. To do so, we selected a high-quality subset of the dataset that covers the best sampled period (1960–2010), in the best sampled areas (Northern Italy to Southern Germany), and only retained the best sampled locations (those with at least 30 y of sampling, >60% temporal coverage). This subset limited our sample size to 3,456 records across 11 locations (SI Appendix, Figs. S9 and S10), compared to 10,858 records across 60 locations used in the full analysis. By doing this, we reduced the problem of varying sampling intensity through time, and also the problem of recent bias toward lower latitudes. We repeated the analysis on this high-quality dataset and produced a simplified version of our model without accounting for the random effect of locations and the sampling effort within these, as these two factors were included in the original model due to the mixed quality of sampling across space (while here we only retain high-quality data). We also found that the number of occurrence records is indeed uneven across species (SI Appendix, Fig. S11); hence, we repeated our analyses after excluding commonly sampled species (those with >50 records). For all tests, GAM models were run using R package “mgcv” (64), while visualization was done using the package “visreg” (65).

To test our hypothesis of climate-induced change in altitudinal homogenization, we measured climate trends in our study region. We extracted the average minimum temperature of the year for each location included our model during the period 1960–2020 (Dataset S2), using Google Earth Engine (66) to access the TerraClimate dataset (67). We then represented the change in temperature over time across locations and estimated global warming ($^{\circ}\text{C}/\text{y}$) in each location as the slope of the linear relationship between temperature and time.

We also performed a species-level analysis to identify the elevational trends in the sampling of individual species. In this case, we wanted to assess whether change in average sampled elevation was different between specialized and generalist feeders and between species living at low or high elevations. In this case, we used all sampling data in our dataset (after the initial filtering for

completeness of spatial and diet information) but only retained 395 species which had at least 10 occurrences sampled over at least 10 y. We divided species into a low-elevation and a high-elevation group, based on the first quartile of the elevation measured across all their occurrences. For each species, we then measured the change in sampling elevation over time, as the slope of a simple ordinary least square regression model. We reported model's slopes registered for species in each diet (polyphagous vs. oligophagous) and elevation (low vs. high) group using histogram plots.

Data, Materials, and Software Availability. The bristle fly dataset used for this analysis is made available here as [Dataset S1](#). The climate data used in this

analysis are made available here as [Dataset S2](#). The R code used for this analysis is made available here as [Appendix S2](#). All other data are included in the manuscript and/or [supporting information](#).

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