Response of insect parasitism to elevation depends on host and parasitoid life-history strategies

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How global warming will affect insect parasitoids and their role as natural enemies of insect pests is difficult to assess within a short period of time. Considering that elevation gradients can be used as analogues for global warming, we carried out meta-analyses of 27 correlations between parasitoid richness and elevation and 140 correlations between parasitism rate and elevation in natural and semi-natural environments. We also explored various covariates that may explain the observed responses. Both parasitism rates and parasitoid species richness significantly decreased with increasing elevation. The decrease was greater for ectoparasitoids and parasitoids of ectophagous insects than for endoparasitoids and parasitoids of endophagous hosts, possibly because these latter are better protected from adverse and extreme climatic conditions occurring at higher elevations. Although our results suggest an increase of parasitism with increasing temperature, other factors regulating herbivorous insects have to be considered before concluding that climate warming will lead to a decrease in pest density.

1. Introduction

Parasitoids play an essential role in regulating insect populations and preventing pest outbreaks. Climate change will affect their action, either through a direct effect on their life cycle or through disturbance of trophic interactions with their host insects and host plants [1,2]. Recent reviews have suggested that climate change will increase the incidence of insect pests, particularly via increased population growth and reduced plant resistance [3]. The same studies pointed out that increasing temperature might also benefit natural enemies and thus negatively affect herbivores but failed to estimate the strength of this top-down effect due to lack of data. Furthermore, life-history traits can affect host and parasitoid species and community responses to climate. For example, we may expect different responses by ecto- versus endoparasitoids (i.e. the larval stage of the parasitoid develops outside or inside the herbivorous host body, respectively) and ecto- versus endophagous hosts (i.e. the larval stage of the herbivorous insect develops externally on the plants or within plant tissues, respectively) because of differences in exposure to weather.

A major issue in studying ecological effects of climate change is the slowness of the process. Ideally, observations should be made over decades, which is rarely possible. Elevation gradients are a powerful tool for testing ecological responses of biota to geophysical influences such as temperature [4], and the influence of changing environment experienced along such gradients has been suggested as analogous to climate warming [5,6]. Hodkinson [6] provided a series of examples where parasitism was measured along elevation gradients. In most cases, parasitism declined with increasing elevation, possibly because of low temperature affecting the survival and behaviour of parasitoids at higher elevations. These
observations are supported by laboratory experiments showing that the functional efficiency of parasitoids decreasing with decreasing temperature [7]. However, studies on the effect of elevation on parasitism and parasitoid complexes have focused mostly on single insect herbivores and their parasitoid complex and did not predict climate change effects on natural enemies in a wide range of ecosystems.

Meta-analyses provide excellent tools with which to recognize common responses of organisms to climate or other ecological variables and to explore covariates explaining the observed patterns [8]. Here, we present the results from meta-analyses testing the hypotheses that parasitism rate and parasitoid richness decrease with elevation. We also test whether the decrease in parasitism rate is greater for ectoparasitoids and parasitoids of ectophagous insects, which are more exposed to variable climatic conditions than endoparasitoids and parasitoids of endophagous hosts.

2. Material and methods

We searched published studies reporting (i) species-specific parasitism rates of herbivorous insects and (ii) species richness of parasitoid complexes of herbivorous insects, at different elevations in bibliographic databases, using the combination of ‘parasit*’ and ‘insect’ and (‘altitud*’ or ‘elevation*’ or ‘mountain’). We also surveyed the references cited in the relevant articles and unpublished CABI reports.

Studies were included in the meta-analyses if they met the following criteria: (i) parasitism rates were reported by individual parasitoid species or genus, or number of parasitoid species, in at least four different elevations separated by a distance of less than 250 km with elevation range of more than 300 m, or a distance of less than 50 km with elevation range of more than 100 m; (ii) parasitism rates were based on at least 10 individuals; (iii) parasitoid and host species were native to the study area and studies were carried out in a natural or semi-natural ecosystem (grasslands, scrublands or woodlands) to capture natural responses to elevation; and (iv) parasitoid richness varied among elevations by at least two species.

This resulted in the selection of 32 publications that accounted for 140 parasitoid species-specific responses to elevation gradients and 20 publications that reported on parasitoid species richness changes along 27 elevation gradients (see the electronic supplementary material, appendix S1 and references in appendix S2). Most of the studies were from central Europe, reflecting a lack of data from other regions in the world, notably in the tropics (electronic supplementary material, appendix S3).

In many cases, the parasitism rates of several parasitoid species were reported for the same insect herbivore within the same elevation gradient. These particular response patterns are not truly independent. We therefore calculated averaged effect sizes at the insect herbivore \\
paralyzes the host and thereby prevents any further development of the host) and the range of elevations (difference between the highest and the lowest elevations).

We tested the effect of four covariates on the magnitude of the relationship between parasitism rate or parasitoid species richness and elevation: (i) herbivore-feeding strategy: herbivorous hosts of the parasitoids were defined as ‘ectophagous’ (e.g. chewers, skeletonizers, leaf-rollers, leaf-tiers and sap-feeders) or ‘endophagous’ (e.g. leaf-miners, gall-makers, cone, seed and fruit insects, bark and root borers); (ii) parasitoid-feeding strategy: parasitoids were classified as ‘ectoparasitoids’ or ‘endoparasitoids’; (iii) latitude of the lower median step of the elevation gradient; (iv) mean annual temperature of the mean elevation of the gradient, extracted from the WorldClim database at 1 km spatial resolution [10]. To avoid problems associated with confounding factors, we tested hierarchically the effect of parasitoid-feeding strategy within each type of host-feeding strategy and then the effect of latitude and temperature within the four categories of host \\

We also tested other attributes for each parasitoid species, including host stage attacked or killed (egg, larval, pupal and adult), parasitoid taxonomy (Diptera versus Hymenoptera), development mode of parasitoid (koinobiont, i.e. parasitoid that allows the host to continue its development after being parasitized versus idiobiont, i.e. parasitoid that permanently paralyses the host and thereby prevents any further development of the host) and the range of elevations (difference between the highest and the lowest elevations).

We used a mixed-effect model to assess between-class heterogeneity (for each categorical covariate, i.e. host and parasitoid types) and to evaluate the significance of the class effect [12], assuming a fixed effect across classes and a random effect within classes [9]. The weighted mean effect size and a bias-corrected bootstrap confidence interval (CI) were then calculated for each class of covariate. Effects were considered statistically significant if the 95% bias-corrected bootstrap CI calculated with 9999 iterations did not include zero. We checked the dataset for publication bias with the weighted Rosenthal’s fail-safe number [13] and normal quantile plots to identify abnormalities in data structure. All meta-analyses were conducted with Metawin v. 2.0 software [14].

3. Results

The species richness of insect parasitoids significantly decreased with increasing elevation ($r_{\text{grand mean}} = -0.31; \text{CI} = -0.53 \text{ to } -0.12$; figure 1). The mean slope of regression across the 27 elevation gradients was significantly negative ($b_{\text{grand mean}} = -
-0.21; CI = −0.38 to −0.07), indicating the average loss of one species of parasitoid every 475 m.

The meta-analysis of the 140 parasitism rates of individual parasitoid species along elevation gradients also revealed that 61 per cent of the correlations were negative (electronic supplementary material, appendix S1). The mean correlation and slope value across all studies were significantly negative ($r_{\text{mean}} = -0.22$; CI = −0.35 to −0.08 and $b_{\text{grand mean}} = -0.21$; CI = −0.35 to −0.08). The normal quantile plot identified no outliers, which means that data can be assumed to come from a single normal distribution, and no gap around zero, indicating the absence of publication bias (electronic supplementary material, appendix S4b). The high Rosenthal’s number (1082), which was about 1.5 times the conservative value of 710, confirmed the absence of publication bias.

The mean coefficient of correlation between parasitism rate and elevation was more than twice as negative for ectophagous ($r_{\text{mean}} = -0.37$) as for endophagous insect herbivores ($r_{\text{mean}} = -0.14$) and for ectoparasitoids ($r_{\text{mean}} = -0.32$) as for endoparasitoids ($r_{\text{mean}} = -0.14$). The effect of the combination of the two covariates on the coefficient of correlation was significant (d.f. = 3, QB = 10.8, $p = 0.01$). Although not significantly different (d.f. = 3, QB = 132.6, $p = 0.13$), the slopes of regression between parasitism and elevation followed the same pattern (figure 2). Only those involving ectophagous insect herbivores were significantly negative, with a steeper slope for ectoparasitoids parasitizing ectophagous herbivores than for endoparasitoids parasitizing endophagous herbivores. The weighted mean slope for parasitoids of ectophagous herbivores corresponded to a loss of ca −0.44 per cent of parasitism per 100 m for a median parasitism rate of 3.7 per cent in the 140 case studies (figure 2). We never observed any significant effect of latitude and mean annual temperature on parasitism rate or parasitoid richness (electronic supplementary material, appendix S4c,d).

None of the other species-related covariates, including host stage attacked or killed, parasitoid taxonomy, development mode of parasitoid and range of elevation, had any significant effect on the correlations between parasitism rate and elevation when tested within each combination of herbivore × parasitoid-feeding strategies.

4. Discussion

These meta-analyses provide the first quantitative evidence that insect parasitism and parasitoid richness generally decrease with elevation. They show a decrease in parasitism rate of ectophagous herbivores of 0.44 per cent per 100 m elevation, which represents a relative loss of ca 15 per cent per 100 m (when related to a median species-specific parasitism rate of 3.7%). Considering that a parasitoid complex is often composed of a large number of species, the cumulative effect of decreasing species-specific rates of parasitism is likely to result in significantly higher host survival.

Our analysis also shows that the decrease with elevation was greater in ectoparasitoids and parasitoids living in or on ectophagous hosts, whereas endoparasitoids of endophagous hosts did not show any reduction in parasitism. This may be due to a better protection by endoparasitoids and parasitoids of endophagous hosts against adverse or extreme weather conditions. It is also possible that, as ectoparasitoids are usually more generalist than endoparasitoids [15], they may be more affected by the possible absence of their alternative hosts at higher elevations [16]. Unfortunately, the available information on parasitoid host ranges is largely unreliable and so the influence of parasitoid specificity on the response to climate change could not be tested.

Parasitism often depends positively on host density [17]. Consequently, it cannot be ruled out that the general decrease in parasitism is caused by decreases in host density. In most cases, host density was not indicated in the studies used for the meta-analyses and, thus, this variable could not be tested. Although reviews [6] suggest that responses of herbivores to elevation are largely idiosyncratic, with different species showing increasing, declining or no elevational trends in abundance, host density affects parasitism and needs to be considered in further studies on the effect of climate change on parasitoids.

Figure 2. Effect of the feeding strategy of insect parasitoid (ecto- versus endoparasitoid) and insect herbivore host (ecto- versus endophagous) on mean slopes of linear regressions between parasitism rate and elevation. Lines represent the weighted mean value of slopes. Shaded areas represent the bias-corrected bootstrap confidence intervals of mean slopes.

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- $r_{\text{mean}}$: Mean correlation coefficient
- CI: Confidence interval
- $b_{\text{grand mean}}$: Grand mean slope coefficient
- QB: Quadratic form of Brownian motion
While a decrease in temperature is the most consistent environmental response to increasing elevation, other factors can be affected as well [4]. Other climate variables such as precipitation, mist, atmospheric turbulence and wind speed change with elevation, but the analogy between elevation and climate change is less straightforward for these variables than for temperature. Harsh weather conditions encountered at higher elevation may affect matting, host foraging and oviposition behaviour in adult parasitoids [18], but the fact that endoparasitism of endophagous insects does not seem to decline at higher elevations suggests that the effects of weather conditions on adults may not be the main driver. In an analysis of climatic factors affecting parasitism of Lepidoptera along a latitudinal gradient, Stireman et al. [19] found that parasitism was mainly driven by precipitation, with parasitism decreasing as yearly precipitation variability and drought periods increase. However, annual precipitation is less likely to vary in elevation gradients than in latitudinal gradients.

Another limitation of our study is that the vast majority of the gradients included in the meta-analyses are situated in central and northern Europe, in particular in the Alps. While this largely reflects the absence of such studies in other continents, it is not clear whether the same patterns would have been found on tropical or subtropical gradients where climate is less seasonal [4] and thermal tolerance of insects to extreme temperatures is usually lower [20].

Our analysis provides a quantitative contribution to the debate on the effect of climate warming on insect pests and their control by natural enemies [3]. It also reveals that host and parasitoid-feeding strategies can be used to build up functional groups showing similar responses to climate change. However, parasitoids are only one group of natural enemies regulating herbivorous insect populations, and further investigations are needed to evaluate the responses of predators and pathogens to climate change.

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References