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Climate and food resources shape species richness and trophic interactions of cavity-nesting Hymenoptera

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Abstract

Aim: Temperature, food resources and top-down regulation by antagonists are considered as major drivers of insect diversity, but their relative importance is poorly understood. Here, we used cavity-nesting communities of bees, wasps and their antagonists to reveal the role of temperature, food resources, parasitism rate and land use as drivers of species richness at different trophic levels along a broad elevational gradient.

Location: Mt. Kilimanjaro, Tanzania.

Taxon: Cavity-nesting Hymenoptera (Hymenoptera: Apidae, Colletidae, Megachilidae, Crabronidae, Sphecidae, Pompilidae, Vespidae).

Methods: We established trap nests on 25 study sites that were distributed over similar large distances in terms of elevation along an elevational gradient from 866 to 1788 m a.s.l., including both natural and disturbed habitats. We quantified species richness and abundance of bees, wasps and antagonists, parasitism rates and flower or arthropod food resources. Data were analysed with generalized linear models within a multi-model inference framework.

Results: Elevational species richness patterns changed with trophic level from monotonically declining richness of bees to increasingly humped-shaped patterns for caterpillar-hunting wasps, spider-hunting wasps and antagonists. Parasitism rates generally declined with elevation but were higher for wasps than for bees. Temperature was the most important predictor of both bee and wasp host richness patterns. Antagonist richness patterns were also well predicted by temperature, but in contrast to host richness patterns, additionally by resource abundance and diversity. The conversion of natural habitats through anthropogenic land use, which included biomass removal, agricultural inputs, vegetation structure and percentage of surrounding agricultural habitats, had no significant effects on bee and wasp communities.

Main conclusions: Our study underpins the importance of temperature as a main driver of diversity gradients in ectothermic organisms and reveals the increasingly important role of food resources at higher trophic levels. Higher parasitism rates at

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higher trophic levels and at higher temperatures indicated that the relative importance of bottom-up and top-down drivers of species richness change across trophic levels and may respond differently to future climate change.

KEYWORDS

antagonists, bees, bottom-up and top-down control, elevational gradients, feeding guilds, land-use change, species richness, trophic levels, wasps

1 | INTRODUCTION

A fundamental goal in ecology is to understand the origin and distribution of species. Patterns of biodiversity have been studied for more than three centuries, giving rise to a number of environmental predictors of broad-scale diversity gradients including climate, energy resources and top-down control (Gaston, 2000; Peters et al., 2016). In addition to environmental filters, biotic interactions such as competition for resources, top-down regulation by antagonists or dependence on mutualistic partners play a role for the occurrence of species (Hunter & Price, 1992; Steffan-Dewenter & Schiele, 2008; Vidal & Murphy, 2018). For example, species with more efficient resource use or better escape strategies to deal with predatory pressure might outcompete species which are less well adapted to local environmental conditions (Kraft et al., 2015). However, the factors which determine the relative importance of one predictor over another remain scarcely understood.

In ecological theory, energy resources are often cited as important drivers of biodiversity (Hurlbert & Stegen, 2014). Ecosystems, with a higher amount of available energy in the form of resources, maintain larger populations with lower extinction risks, and thus higher biodiversity (Srivastava & Lawton, 1998). Apart from the abundance of resources, the diversity of food resources may be closely linked to species diversity as a high diversity of food resources offers more distinct niches for concomitant speciation processes to take place (Forbes, Powell, Stelinski, Smith, & Feder, 2009). While the availability of resources has repeatedly been found to be positively correlated with species richness for endothermic taxa (Buckley, Hurlbert, & Jetz, 2012; Ferger, Schleuning, Hemp, Howell, & Böhning-Gaese, 2014), its relevance for ectotherms is more variable and depends on consumer groups, tropic level and habitat type (Schuldt et al., 2019). Furthermore, climate impacts ectotherms by limiting resource acquisition at low temperatures. In ectothermic organisms, food resource availability is often not proportional to food resource intake, as foraging is only possible within certain temperature thresholds (Classen et al., 2015; Willmer, 1983).

Another approach assumes that biodiversity is primarily maintained by top-down control of natural antagonists, that is, predators, cleptoparasites and parasitoids. The presence of antagonists restricts competition and therefore the dominance of a few species, thereby allowing coexistence (Terborgh, 2015). This hypothesis, proposed in 1960 (Hairston, Smith, & Slobodkin, 1960), was further developed by Janzen and Connell in their theories on negative density dependence of mortality agents, which include parasites and pathogens (Connell, 1970; Janzen, 1970). Empirical evidence for the importance of top-down control for the maintenance of species diversity, however, is still mainly limited to plant communities and vertebrate top predators (Bagchi et al., 2014; Terborgh, 2015).

Ecologists have emphasized the notion of temperature as the dominating factor promoting species richness, in particular for ectothermic taxa (Buckley et al., 2012). First, temperature is assumed to directly confine species richness via physiological constraints since only a few species can tolerate harsh climatic conditions at high elevations and latitudes (Currie, 1991). Second, the exploitation of resources is thought to be temperature dependent (Brown, 2014). Third, temperature affects biodiversity indirectly through the acceleration of ecological processes such as biotic interactions (Brown, 2014) and fourth, temperature affects evolutionary processes through increasing rates of diversification (Van Valen, 1973).

Human land use is regarded as an important driver of diversity loss and has reshaped mountain ecosystems (Peters et al., 2019). It reflects the anthropogenic impact through disturbance and conversion of natural habitats into agricultural habitats and subsequent land-use intensification (Laurance, Sayer, & Cassman, 2014; Newbold et al., 2015). Land use has been shown to have direct negative effects on the biodiversity of insect communities (Martinson & Fagan, 2014).

Past studies have yielded different results as to whether climate or resources are of greater importance as a driver of diversity (Buckley et al., 2012; Ferger et al., 2014). An important factor in this respect might be the trophic level of the studied organisms. Energy is lost through respiration and metabolic heat production from one trophic level to the other (Brown, 2014). Therefore, the availability of resources might have a stronger impact on higher trophic levels via cascading effects. Other cascading effects might be also driven by temperature because temperature modulates the magnitude of the impact of higher trophic levels on lower ones (Rodríguez-Castañeda & Sykes, 2013). Moreover, higher trophic levels respond differently to land-use changes than lower trophic levels (Barnes et al., 2017) and higher trophic levels seem to be the most sensitive to anthropogenic disturbance (Ewers & Didham, 2006).

We installed trap nests along an elevational gradient at Mt. Kilimanjaro (Tanzania) to investigate the combined effects of resources, top-down control by antagonists, climate and land use on species richness at different trophic levels. Trap nests are an excellent model system for studying cavity-nesting insect communities

which serve as good bio-indictors for habitat quality and environmental change (Tscharntke, Gathmann, & Steffan-Dewenter, 1998). They provide a means of assessing the influence of drivers of diversity on hymenopterans at different trophic levels. In addition to the diversity of individual trophic levels, resource diversity for the higher trophic levels can be quantified and top-down control measured; data which are often hard to capture for other insect functional groups. Cavity-nesting bees and wasps provide pollen, caterpillars or spiders as food for their offspring and sustain a large number of different antagonist guilds, which predate or parasitize host larvae or use their food provisions (Wcislo & Cane, 1996). Tropical mountain ecosystems, such as Mt. Kilimanjaro, are ideal systems for studying biodiversity patterns under different environmental conditions, as they provide elevational gradients with changing climate, ecosystem structure and availability of resources at small spatial scales (Sanders & Rahbek, 2012). Furthermore, the study region is particularly interesting as the evolutionary origin of bees took place here (Danforth, Brady, Sipes, & Pearson, 2004; Hedtke, Patiny, & Danforth, 2013; Michener, 2007).

Our work thus tests the following non-exclusive hypotheses:

Hypothesis 1 *Food resource quantity and diversity enhance species richness. Resource-poor habitats support a lower number of herbivores and therefore offer a lower amount of resources to sustain predator populations (Steffan-Dewenter & Schiele, 2015). Hence, we assume that resources are more limiting at higher trophic levels.*

Hypothesis 2 *Top-down control is an important factor shaping species diversity by reducing the competitive advantage of potentially dominant species (Terborgh, 1998). Thus, we expect predation pressure, here parasitism rate, to enhance species richness if resource availability is not limiting species richness.*

Hypothesis 3 *Higher temperatures accelerate ecological and evolutionary rates (Brown, 2014), facilitating the evolution and maintenance of a higher level of diversity in ectothermic organisms. Therefore, we expected positive correlations between temperature and species richness, as well as parasitism rates on all trophic levels in the cavity-nesting community.*

Hypothesis 4 *Land use has more severe negative effects on arthropod species richness at higher trophic levels (Attwood, Maron, House, & Zammit, 2008). Therefore, we expect lepidopteran- and spider-hunting wasps and their respective antagonists to be more affected by land use than bees and their dependent antagonists.*

2 | METHODS

2.1 | Study area and design

The study was conducted at Mt. Kilimanjaro, the highest free-standing mountain of the world. It covers an elevational gradient from 700 to 5,895 m a.s.l. and consequently a diverse number of ecosystem types in different elevational belts. The mean annual temperature decreases by ~0.56°C per 100 m; from 25°C in the lowlands to −8°C at the summit (Appelhans et al., 2016). Mean annual precipitation exhibits a hump-shaped elevational distribution and peaks in the forest belt at ~2,200 m a.s.l. (Appelhans et al., 2016). Based on a pilot study which showed that cavity-nesting Hymenoptera were limited to elevations below 1,800 m a.s.l, that is, lower than the forest belt (see Appendix S1), we selected 25 study sites of 50 × 50 m in the lower elevations on the southern and south-eastern slopes of Mt. Kilimanjaro (3°10'–3°23'S, 37°14'–37°41'E). The study sites ranged from 866 to 1,788 m a.s.l., had a temperature gradient of 5.6°C (Figure S2.1 in Appendix S2) and covered the five major natural and disturbed ecosystem types, with four to six replicates in each, of this elevational range. The lowest elevations included shrub savannahs as natural, and maize fields as disturbed ecosystems. In the mid-elevations, we compared three disturbed ecosystem types with different land-use intensities: diverse agroforestry systems of the local Chagga tribe (Chagga homegardens), extensively managed grasslands and coffee plantations.

The species richness of stem-nesting bees, crabronid, eumenid, sphecid and pompilid wasps and their antagonists, was assessed with trap nests (Figure 1, Figure S2.2d in Appendix S2). In total, we installed 208 trap nests at ground and canopy level (eight traps per site, arranged in four paired trap nests; Figure S2.2a,b,c in Appendix S2). Trap nests were operated for 15 months and checked monthly for new occupants. Internodes filled with nests were replaced by new internodes. All collected internodes filled with nests were taken out of the trap nests, closed with metal nets and reared on the study sites in hatching boxes (Figure S2.2a in Appendix S2) so that the climatic conditions were natural during the whole development of the larvae. After hatching, nests were cut open in the laboratory to count the number of brood cells and measure parasitism rate (Figure S2.2e,f in Appendix S2). All specimens were identified to the level of morphospecies or species whenever possible. We used additional taxonomic literature for the closer identification of wasp clades and bee species (identification keys for bees Table S3.1 in Appendix S3). Hosts and antagonists were identified to different taxonomic depths. Whereas the host guilds were identified to morphospecies level, some antagonist groups, like the Chrysididae could not be separated further. Trap-nest data were pooled per study site.

2.2 | Species richness of cavity-nesting bees, wasps and their antagonists

We assessed species richness of functional groups of different trophic levels: herbivores, that is, pollen and nectar feeders (bees: Apidae, Colletidae, Megachilidae), predatory wasps (caterpillar-hunting: Eumeninae and spider-hunting wasps: Pompilidae, Sphecidae, Crabronidae) and their respective antagonists and second-order antagonists (hyperparasitoids; Figure 1). Species richness was calculated as the total number of species observed per study site. As the sampling of insects is rarely complete and differences in sampling completeness can lead to biases, we estimated the asymptotic

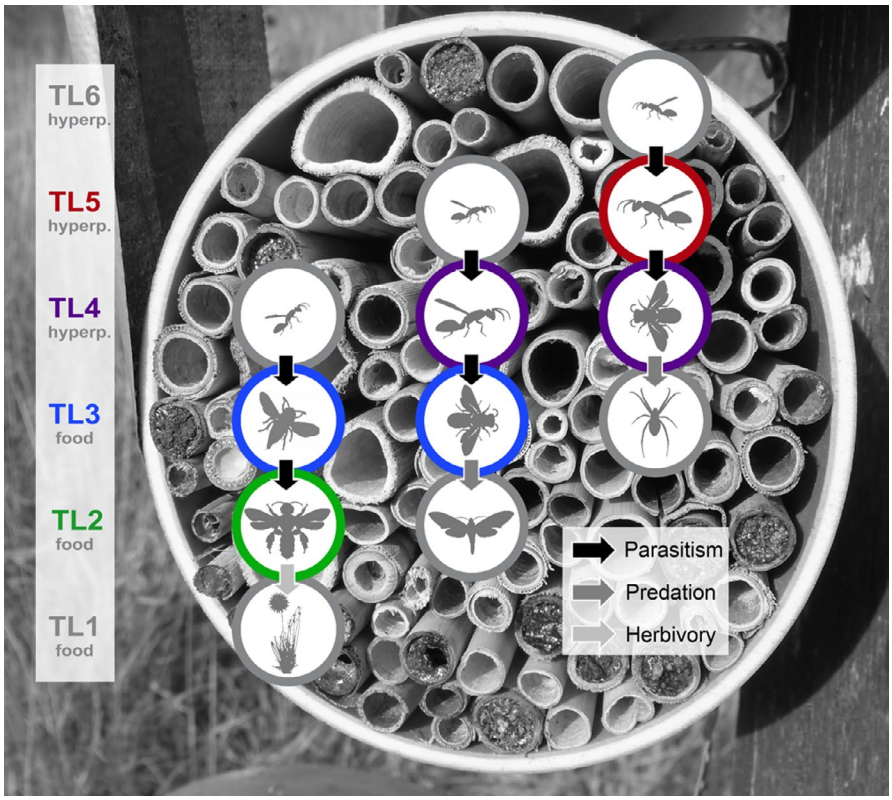

FIGURE 1 Sketch showing the cavity-nesting community at Mt. Kilimanjaro. Three different functional groups of hosts: pollinators (Apidae, Colletidae and Megachilidae), caterpillar-hunting predators (Eumeninae) and spider-hunting predators (Pompilidae, Sphecidae and Crabronidae) with their antagonists, food resources and interaction types are displayed. Parasitism is here also used for parasitoidism, which was the case for most parasitized brood cells. It was counted as all occurrences in which the host had been killed. Arrows indicate the type of top-down effect. Colours indicate the trophic level affiliation. Functional groups with a colourful circle display the groups for which we analysed species richness patterns. TL: trophic level

species richness with the sample-based estimator Chao (Chao, 1984, 1987), using the function 'ChaoRichness' in the *iNEXT* package in R (Hsieh, Ma, Chao, & McInerny, 2016). Chao1-estimated species richness and observed species richness correlated strongly in all host groups (Pearson correlation coefficient between $r = .90$ and $r = 1.00$). We were able to collect 89%–100% of the estimated species of local cavity-nesting communities. The proportion of observed to estimated species richness showed no correlation pattern with elevation, so we can assume that the sampling was equally comprehensive at all elevations. Therefore, we used the observed species richness instead of the estimated species richness in our models. Host species with low abundances and species richness, such as aphid-hunting wasps, cicada-hunting wasps and orthopteran-hunting wasps, which were also found in trap-nests, were excluded from the analysis (Table S3.2 in Appendix S3).

2.3 | Temperature, land use, resource data and parasitism rate

Temperature was recorded with temperature sensors for 23 study sites in 5-min intervals between 2011 and 2014 and the mean annual temperature (T) was calculated per study site as the average of temperature values (Appelhans et al., 2016). For two study sites, where data loggers were lost, we used a co-kriging approach to estimate missing data (Appelhans et al., 2016). We used a composite land-use index (LUI) to quantify the anthropogenic impact on ecosystems. The LUI is described in detail in Peters et al. (2019) and is based on standardized measurements of four land-use components which were quantified at both the site (annual removal of plant biomass, agricultural inputs to the ecosystem, the vegetation structure in comparison to the natural habitats) and landscape level (proportion of agricultural land in the surrounding landscape of the study sites). Annual removal of plant biomass and agricultural inputs (e.g. fertilizer, pesticide use) were estimated by repeated visits of the study sites and information from local landowners. The vegetation structure was quantified as the dissimilarity to the natural vegetation at the same elevation. It was composed of measurements of canopy closure, canopy height and spatial vegetation heterogeneity. For the estimation of agricultural land in the surrounding landscape (at a radius of 1.5 km), ASTER imagery by the Terra satellite with a spatial resolution of 15–90 m was classified into 27 different land cover types (18 natural and nine managed habitat types). The proportion of agricultural land was calculated using these data. The four land-use components were standardized and equally weighted to calculate a mean value of land-use intensity (i.e. the LUI). The trends in temperature and land use along the elevational gradient are shown in (Figure S4a,b in Appendix S4). The Pearson correlation coefficient between temperature and LUI was $r = -.36$ so that we were able to use them as independent variables. Resources for each functional group, that is, flowers, moths, spiders, bee and wasp hosts, were recorded separately, and we assessed resource quantity as well as resource diversity (Appendix S5). The parasitism rate was calculated as the number of brood cells in which the host had been killed in relation to the total number of brood cells of the respective host group. The hyperparasitism rate, used in the models as parasitism rate of the antagonists, was calculated as the number of brood cells

in which the antagonists had been killed by second-order antagonists in relation to the number of parasitized brood cells.

2.4 | Statistical analysis

We used generalized additive models (gam) as implemented in the R package 'mgcv' (Wood, 2019) to calculate trends in species richness of bees, caterpillar-hunting and spider-hunting wasps and their respective antagonists along the elevational gradient. In case of species richness as the response term, the data family was set to 'poisson' or 'quasipoisson' (in case of overdispersion) to account for the properties of count data. In gam models, we set the basis dimension of the smoothing term k to four to avoid over-parameterization of trend functions (Peters et al., 2016). Trend lines derived with gams were only plotted if the significance level of the elevation term was $p < .05$. In case of parasitism rates, the data family was set to 'binomial' and the trends in parasitism rates were calculated with a logit link-function.

We hypothesized that the species richness of cavity-nesting Hymenoptera is driven by temperature, land use, resource quantity and diversity, and predation pressure in the form of parasitism. We used generalized linear models (glm) with a 'poisson' or 'quasipoisson' distribution, respectively, to test the additive effects of temperature, land use, resource quantity and diversity and parasitism rate on species richness for each functional group (Table S6 in Appendix S6). We controlled for collinearity with Pearson correlation coefficients (Figure S6 in Appendix S6) and used $r > .7$ as a threshold (Dormann et al., 2013). Pearson correlations coefficients with $r > .7$ only occurred in some models between resource abundance and resource richness. Resource abundance naturally affects resource richness and belongs to the same hypothesis (H1). In two of three cases, the Pearson correlation coefficients were only slightly > 0.7 and we analysed them together in our models because we were interested whether resource abundance or resource richness affect the consumer's species richness stronger.

To test whether the magnitude of identified drivers of species richness was linked to the trophic levels, we also calculated a linear mixed effect model (lme) with study site as random factor and tested for possible interactions between the explanatory variables and the trophic level. Previously, species richness and resource richness and abundance were z-transformed per functional group:

$$z = \frac{\chi - \mu}{\sigma},$$

where χ is the raw score, μ is the mean score of the functional group and σ is the standard deviation of the functional group.

We used the 'dredge' function of the *MuMIn* package (Bartón, 2018) in R to evaluate the support for the full model and all nested models. Models were ranked according to their Akaike information criterion corrected for small sample sizes (Burnham & Anderson, 2004) and delta distances to the next best model were calculated. In cases of quasi models, we calculated a QAICc instead of the normal AICc (Bolker, 2017). Before the analyses, all explanatory variables were standardized by z-transformation, using the 'scale' function in R to facilitate the comparability of their effect strength. While we concentrate our inference on the best supported model, all models with ΔAICc < 3 or ΔQAICc < 3, respectively, are presented in the Supplementary Information. In addition, we performed multi-model averaging, using the 'model.avg' function in R.

Because parasitism rate could not be calculated for sites where the respective host guild did not exist and resource data for spider-hunting wasps was not available for all study sites, some models could not be evaluated with data from all study sites. Therefore, we recalculated the models without parasitism rate and in the last step without resource availability to include all study sites and therefore enhance the statistical power of the models.

For each host guild, we further tested with generalized linear models (glm) with a binomial data distribution (and quasibinomial distribution in the case of overdispersion) whether parasitism rates were affected by temperature and land use.

3 | RESULTS

3.1 | Elevational patterns of species richness and parasitism rate

In total, we found 4,051 nests of stem-nesting bees and wasps, containing 14,937 brood cells of 81 morphospecies of hosts (38 bee and 43 wasp morphospecies) and 49 morphospecies of antagonists (Table S7.1, S7.2 in Appendix S7). Cavity-nesting Hymenoptera exponentially declined with elevation and were generally limited to elevations below 1,800 m a.s.l. (Figure S1). Species richness patterns of cavity-nesting hosts differed between bees, caterpillar-hunting wasps and spider-hunting wasps and their respective antagonists. While bees and their antagonists, as well as the antagonists of the caterpillar-hunting wasps declined monotonically (Figure 2a,b), caterpillar- and spider-hunting wasps and the antagonists of the spider-hunting wasps showed an increasingly humped-shaped elevational distribution as the trophic level increased (Figure 2b,c).

The parasitism rate differed between the different trophic levels and almost doubled from one level to another from 12% in bee nests to 24% in caterpillar-hunting wasp and 45% in spider-hunting wasp nests. The hyperparasitism rate also increased as the trophic level increased (Figure 3a). The parasitism rate decreased with elevation across all host groups, as did the ratio of antagonist to host species (Figure 3b,c) while hyperparasitism rate showed no significant pattern (Figure S8.1 in Appendix S8). The parasitism rate was positively correlated with temperature for caterpillar-hunting predators and negatively correlated with land use for pollinators (Table 1, see Table S8.2 in Appendix S8 for competitive models).

3.2 | Drivers of species richness

We hypothesized that temperature, food resources and top-down control by antagonists drive species richness of cavity-nesting

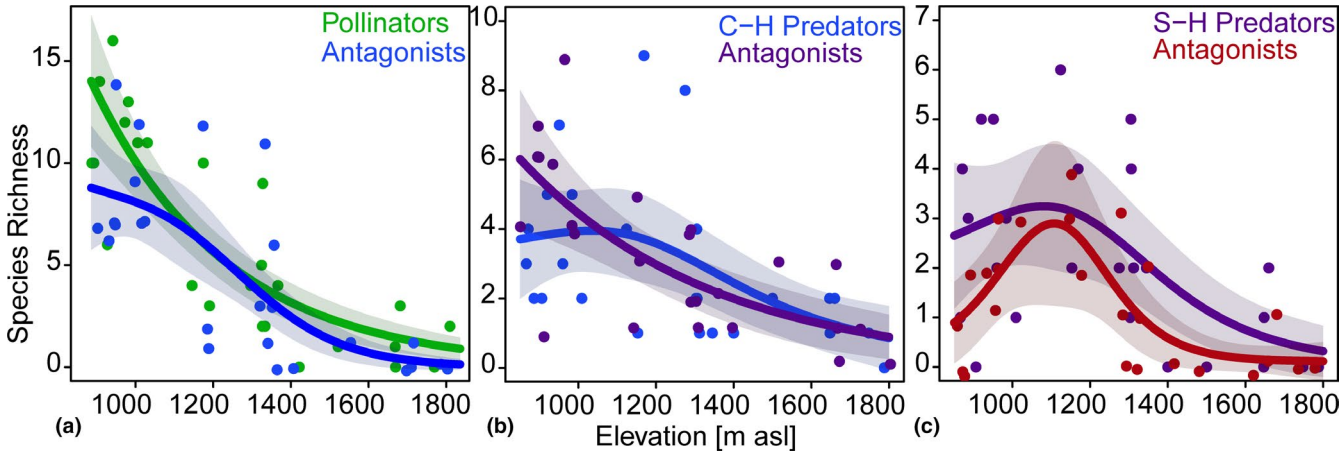

FIGURE 2 Patterns of elevational species richness of three different cavity-nesting host guilds and their respective antagonists at Mt. Kilimanjaro. Generalized additive models were used to estimate trends of elevational richness (Poisson family, basis dimension (k) = 4). Species richness significantly changed for all insect groups with elevation (a: pollinators: explained deviance (ED) = 68.1%, $p < .001$; antagonists of bees: ED = 57.9%, $p < .001$; b: caterpillar-hunting wasps: ED = 31.5%, $p = .01$; antagonists of caterpillar-hunting wasps: ED = 48.4%, $p < .001$; c: spider-hunting wasps: ED = 34.5%, $p = .01$; antagonists of spider-hunting wasps: ED = 47.4%, $p = .01$). Colours indicate trophic level affiliations

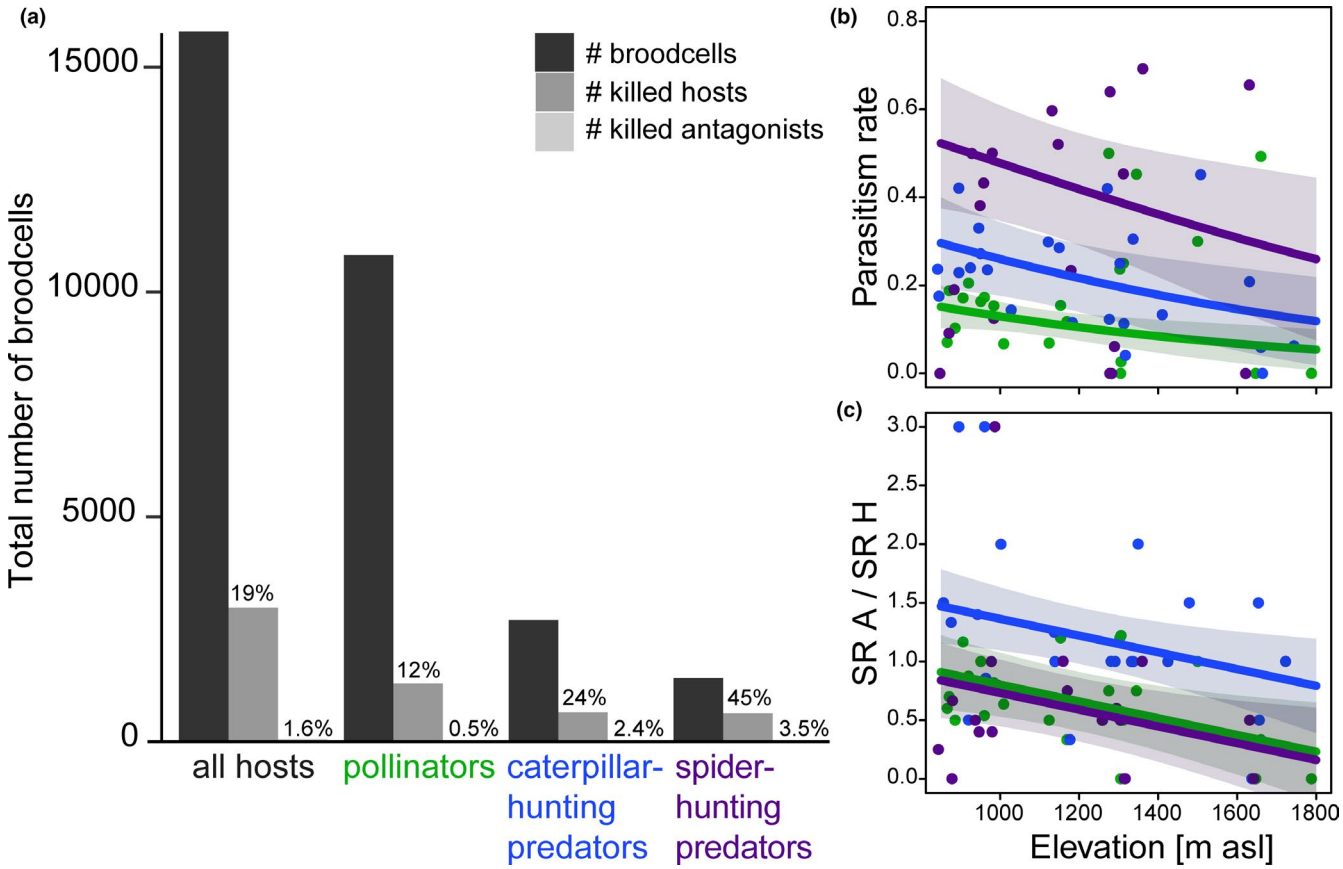

FIGURE 3 Parasitism of trap nests at Mt. Kilimanjaro. (a) Parasitism and hyperparasitism rates changed among functional groups. The barplots display the total number of brood cells (black), the number of brood cells in which the host was killed by the antagonist (grey, deadly parasitism also indicated above the bars as the percentage of the total number of brood cells in which the host was killed), and the number of brood cells in which the antagonist had been killed (light grey, deadly hyperparasitism also indicated above the bars as the percentage of the total number of parasitized brood cells). (b) Parasitism rates of functional groups vary along the elevational gradient (dots). The mean parasitism rate correlated significantly with elevation (GLM with quasibinomial data family, $p_{elevation} = 0.045$, lines). (c) The number of antagonist species in relation to the number of host species correlated significantly with elevation (LM $p_{elevation} = 0.013$, lines). SR A: Species richness of antagonists; SR H: Species richness of hosts. Colours indicate the trophic level affiliation

TABLE 1 Best models explaining the parasitism rate of cavity-nesting Hymenoptera at different trophic levels at Mt. Kilimanjaro, derived by QAICc values

Parasitism rate	T	LUI	QAICc	Weight	ED	# Sites
Pollinator		−0.40	22.2	0.49	0.27	22
Caterpillar-hunting predator	0.47		40.9	0.67	0.25	24
Spider-hunting predator			31.9	0.51	0	19

Note: For T and LUI standardized beta values from best-fit GLM models are shown. Colours indicate positive significant values (blue) and negative significant values (red).

Abbreviations: # Sites: number of sites taken into account for the model; ED, explained deviance; LUI, land-use index [value between 0 and 1; 0 = lowest land use; 1 = highest land use]; T, mean annual temperature [°C].

TABLE 2 Best models explaining species richness of hosts and antagonists of cavity-nesting Hymenoptera at Mt. Kilimanjaro derived by AICc/QAICc-based model selection

Guild	Functional group	TL	T	LUI	RES-AB	RES-RI	ED	# Sites
Host	Pollinator	2	0.77				0.59	25
Host	Caterpillar-hunting predator	3	0.30				0.14	25
Host	Spider-hunting predator	4					0.00	14
Antagonist	Pollinator	3	0.48		0.34	0.45	0.76	25
Antagonist	Caterpillar-hunting predator	4	0.43		0.31		0.62	25
Antagonist	Spider-hunting predator	5				0.69	0.40	25

Note: Standardized parameter estimates from best-fit models. Please note that parasitism rate was not included as an explanatory variable here because of a lower sample size. Blue indicates significant positive standardized beta values as calculated with GLM models (no negative correlations were found).

Abbreviations: # Sites, number of sites taken into account for the model. Best models including parasitism rate as an explanatory variable are shown in Table S9.1 in Appendix S9; ED, explained deviance; LUI, land-use index [value between 0 and 1; 0 = lowest land use; 1 = highest land use]; RES-AB, abundance of resources [mean number of flowers, butterflies, spiders, bees or wasps]; RES-RI, species richness of resources [total number of observed (morpho)species of resources]; T, mean annual temperature [°C]; TL, trophic level.

Hymenoptera and expected stronger effects of land use at higher trophic levels. While we found no support for an effect of land use and top-down control (parasitism), both mean annual temperature and resource quantity and richness were important predictors of the diversity of cavity-nesting host and antagonist communities (Table 2). The strongest positive effect of temperature was found for bee richness (ED = 0.59, $p_{temperature} < 0.001$). Caterpillar-hunting wasps and their antagonists showed a less significant correlation with temperature, whereas richness patterns of spider-hunting wasps and their antagonists were not explained by temperature (Table 2). Resource variables were not supported as predictors of host species richness, although their importance increased at higher trophic antagonist levels (Table 2). The species richness of antagonists of bees was best explained by both resource abundance and richness (ED = 0.76, $p_{temperature} = 0.053$, $p_{RES\text{-}AB} < 0.01$, $p_{RES\text{-}RI} < 0.05$). While the species richness of antagonists of caterpillar-hunting predators was predicted by resource abundance (ED = 0.62, $p_{temperature} < 0.01$, $p_{RES\text{-}AB} < 0.001$), the effect of resource richness was more relevant for the antagonists of spider-hunting predators (ED = 0.40, $p_{RES\text{-}RI} < 0.001$) than caterpillar-hunting predators. The competitive models, differed only partially from the best model, the reduced and the full models developed from different subsets of the dataset, are presented in Appendix S9 (Table S9.1 in Appendix S9). Results revealed by multi-model averaging confirmed the relative variable importance of explanatory variables (Table S9.2 in Appendix S9). Testing for possible interactions between the identified drivers of species richness and trophic levels revealed that the interactions between trophic level and resource abundance, as well as trophic level and temperature, were significant (Table S9.3 in Appendix S9).

4 | DISCUSSION

In this study, elevational species richness patterns changed with trophic level from monotonically declining richness of bees to increasingly humped-shaped patterns for caterpillar-hunting wasps, spider-hunting wasps and antagonists. Furthermore, parasitism rates and antagonist–host ratios decreased with elevation and parasitism rates increased with trophic level. Our data indicate that temperature is a dominant factor in shaping diversity patterns with more intense trophic interactions in warmer climates. By systematically analysing different trophic levels, we found that the availability of resources gained more weight as a driver of species richness in antagonist groups than in bee and wasp hosts. Thus, our study provides novel insights into the relative importance of temperature, resources, trophic level and biotic interactions as drivers of elevational diversity patterns for hymenopteran taxa with broad functional relevance.

4.1 | Decline of species richness along the elevational gradient

We found a highly diverse stem-nesting insect fauna with 81 host and 49 antagonist species, in comparison to other trap-nest studies from the tropics where five to eight bee and seven to fifteen wasp species were reported (Klein, Steffan-Dewenter, & Tscharntke, 2006; Perillo, Neves, Antonini, & Martins, 2017; Stangler, Hanson, & Steffan-Dewenter, 2015; Tylianakis, Tscharntke, & Lewis, 2007). One reason for the higher diversity may be the broader climatic amplitude and the coverage of different habitat types in our study. With the exception of Perillo et al. (2017), other studies did not include a significant elevational gradient in their study region. A second reason for the high diversity may be the close proximity to the origin of bees, which goes back to the xeric interior of Gondwana (todays Africa and South America), providing a long time to diverge to current diversity levels (Danforth et al., 2004; Hedtke et al., 2013; Michener, 2007). The decline of bee species richness at higher elevations has already been shown for Mt. Kilimanjaro (Classen et al., 2015), and in other parts of the world (Hoiss, Krauss, Potts, Roberts, & Steffan-Dewenter, 2012; Perillo et al., 2017), whereas studies for wasp taxa are largely lacking (Corcos et al., 2018). We found a humped-shaped decline of both caterpillar-hunting and spider-hunting wasp species richness, with a peak in species richness at intermediate elevations. Depending on the taxonomic group of wasps, other studies either found a distinct decline of species richness or a mid-elevation increase in diversity as was demonstrated for wasps, but ultimately a decline in species richness at highest elevations (Kumar, Longino, Colwell, & O'Donnell, 2009; Perillo et al., 2017). The humped-shaped species richness pattern of wasp taxa at Mt. Kilimanjaro may be due to the increasingly forested habitats at mid-elevations on, and in the areas surrounding of, the study sites, whereas at higher elevations climatic conditions limit the occurrence of many species. For the species richness of antagonists, we found that the higher the trophic level of antagonist, the more the pattern shifts from a monotonous decline of species richness to a mid-elevation peak, following closely the species richness of their hosts. Several other studies evaluated species richness of antagonists along elevational gradients and found variable patterns (Janzen et al., 1976; van Noort, 2004; Noyes, 1989), but a systematic analysis of different trophic levels and the underlying drivers of richness patterns is currently lacking.

4.2 | Temperature drives species richness across trophic levels

In our study, temperature was the most important and only common driver of species richness at all trophic levels. This result confirmed our third hypothesis that species richness at all trophic levels is correlated with temperature and is in line with the pervasive dependence of ectothermic animals on temperature as a pacemaker of metabolism, foraging activity, population growth and diversification (Brown, 2014; Brown, Gillooly, Allen, van Savage, & West, 2004). As we were able to separate the effects of temperature from those of resource availability and top-down control, our results suggest that ecological mechanisms such as temperature-mediated resource exploitation or evolutionary processes such as faster speciation or lower extinctions rates are the underlying temperature-mediated causes of diversity patterns (Buckley et al., 2012; Classen et al., 2015). We are aware that temperature is not independent of elevation and thus co-varying environmental factors, such as precipitation, atmospheric pressure, solar radiation and land area might also influence species richness (Perillo et al., 2017). However, both ecological theory and empirical findings underscore the importance of temperature for the origination and maintenance of diversity gradients, while only very limited evidence exists for a role of the other mentioned environmental factors changing with elevation (Peters et al., 2019, 2016). Nevertheless, other environmental factors, such as rainfall, strongly affect life-history traits of tropical insects (reviewed in Kishimoto-Yamada & Itioka, 2015), yet maybe not species richness. Furthermore, we also found higher parasitism rates and antagonist–host species richness ratios at lower elevations, indicating temperature-mediated interaction strength as a further potential mechanism that allows the coexistence of more species in warmer climates (LaManna et al., 2017; Peters et al., 2016; Terborgh, 2015).

4.3 | Resources become increasingly important for antagonists

In addition to temperature, food resource availability played a major role in explaining the species richness of antagonists. This is consistent with our first hypothesis that higher trophic levels are more limited by food resources than lower trophic levels. Antagonists depend on their hosts, which have to cope with the spatially and temporally limited food resources for their offspring (Godfray, 1994). Therefore, it is very likely that there is a strong selection pressure to use their host resources very efficiently (Sanders, Moser, Newton, & van Veen, 2016). We also hypothesized that the importance of resources for species richness increases with higher trophic levels of host taxa, but we found no correlation between resource availability and diversity of bees and wasp host guilds. One reason for the lack of a correlation could be a higher inaccuracy in our estimates of resources for organisms at lower trophic level. However, flower resources were repeatedly recorded in detail during the whole study phase, allowing rather precise estimates of resource availability for pollinators. Abundance records for moths and spiders were, however, of lower quality. Therefore, for predatory wasps, we cannot fully exclude that the relevance of resources might be higher in reality. Nevertheless, the results confirm an increasing importance of resource availability for antagonists compared to host taxa. Please note that we did not consider other resources than food

on which stem-nesting hymenoptera depend like the availability of nesting sites and nest-building materials. These nest-building materials differ between cavity-nesting species and cover a variable range including clay, chalk, small stones, resins, bark pieces, leaves and plant hair (Krombein, 1967). Flying insects can gather these resources from the surroundings, and woody structures were always within a distance of less than 200 m from the study sites. Therefore, we do not assume that the lack of nesting sites and nest-building materials could have been a limiting factor for species richness in our study.

4.4 | Top-down control of species richness

As mentioned above, our results indicated that more intense trophic interactions occurred in ecosystems with higher temperatures, as found in Forrest and Chisholm (2017), supporting the notion that trophic interactions are sensitive to temperature changes (Deutsch et al., 2008). However, our analyses provided no direct support for top-down control as a mechanism for the maintenance of biodiversity, as the parasitism rate was not a significant explanatory factor in any model with temperature and resources as additional factors. Thus, parasitism rate or hyperparasitism rate as a top-down effect did neither affect the species richness of hosts nor antagonists, contrasting to our second hypothesis. There are several possible explanations for the absence of an effect of predation pressure on species richness: First, top-down control might not be a relevant driver of diversity patterns in our study system. Second, the inclusion of temperature in the models might mask impacts of top-down control due to higher strength of trophic interactions in warmer climates. Third, other top-down factors could be important as well, such as the predation pressure from birds or insectivorous mammals, which we did not include in our evaluation. Fourth, resources might be more limiting than predation pressure in our system as resource availability was a very important explanatory variable for the species richness of antagonists. In this case, one could assume that the effect of resource limitation on species richness was stronger than the effect of predation pressure on species richness. However, significantly higher parasitism rates at higher trophic levels indicate that these species face higher pressure by both resource limitation and top-down predation. Since there are hardly any arthropod studies on this topic, more studies are necessary to disentangle the above-mentioned mechanisms, also testing more specifically for conspecific density-dependent abundance regulation (Forrest & Chisholm, 2017; LaManna et al., 2017; Steffan-Dewenter & Schiele, 2008).

4.5 | Limited effects of land use on species richness

We found no significant effects of land use on species richness of bees, wasps or their antagonists, in contrast to our fourth hypothesis. Previous studies in tropical agroecosystems also found no negative influence of land use on the species richness of cavity-nesting Hymenoptera (Klein, Steffan-Dewenter, Buchori, & Tscharntke, 2002; Tylianakis, Klein, Lozada, & Tscharntke, 2006). Nevertheless, there are other tropical studies which found significant negative effects of land use on the species richness of insects (Perry et al., 2016). In a study with a multi-taxon approach, ranging from microbes to birds, land use had a negative effect on species richness, with increasing magnitude at higher trophic levels (Barnes et al., 2017). On Mt. Kilimanjaro, land use is still moderate with manual tillage and sustainable subsistence agriculture of the local Chagga people (Fernandes, Oktingati, & Maghembe, 1984), forming a mosaic landscape of Chagga agroforestry systems, species-rich, extensively used grasslands and maize fields with many flowering herbs, embedded in natural savannah areas. The distance to the nearest woody habitat has been found to have negative impacts on the number of cavity-nesting species (Klein et al., 2006), but in our study it was less than 200 m to all our study sites. However, ongoing land-use change at Mt. Kilimanjaro, which involves significant losses of savannah areas, replacement of Chagga agroforestry systems by coffee monocultures and general agricultural intensification could become a threat to biodiversity and negatively affect the ecosystem services provided by bees and wasps in this area (Classen et al., 2014; Hemp, 2006).

5 | CONCLUSIONS

In our study, elevational species richness patterns changed with trophic level and were best explained by temperature for host taxa, whereas antagonists were also limited by food resources. Climatic changes will probably affect bees, wasps and their antagonists differently. This might lead to differences in range shifts, changing the composition of communities. Importantly, changes in host species richness patterns will have impacts on whole food webs and might affect the extremely dependent antagonists most severely. Upper thermal limits will first be reached in the most diverse savannah habitats (Barlow et al., 2018), probably leading to species losses in the lower elevations. Furthermore, future risks of land use might be reinforced by combined effects of habitat fragmentation and climate change. On the whole, systematic studies on insect communities at different trophic levels along environmental gradients are still rare and provide, combined with manipulative experiments, a strong model system to better understand environmental factors and biotic interactions as drivers of species richness patterns.

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DATA AVAILABILITY STATEMENT

The processed data are documented and archived in the PANGAEA database at: https://doi.pangaea.de/10.1594/PANGAEA.907535 (Mayr, Steffan-Dewenter, 2019). The R code can be provided upon request.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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