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Seasonal variation in the ecology of tropical cavity-nesting Hymenoptera on Mt. Kilimanjaro

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Abstract

Insect communities vary seasonally with changing climatic conditions and related changes in resource availability, strength of competition, or pressure by natural antagonists. But seasonal dynamics, particularly in tropical mountain ecosystems, are not well understood. We monitored cavity-nesting Hymenoptera communities on Mt. Kilimanjaro, Tanzania, to analyse temporal patterns of nest-building activity, ecological rates, and life-history traits in relation to seasonal climatic variation and elevation. We installed trap nests on 25 study sites in natural and disturbed habitat types covering the colline (<1,300 m) and submontane zones (≥1,300 m a.s.l). We analysed patterns of seasonality in the cavity-nesting ecology of Hymenoptera at three different trophic levels –bees, caterpillar-hunting wasps and spider-hunting wasps– over a complete annual period, covering two rainy and two dry seasons. Nest-building activity showed strong seasonal trends in all three investigated trophic levels and peaked at the end of the short rainy season at low elevations. Nest-building activity was considerably higher and seasonal trends were better synchronised between the different trophic levels in the colline zone at low elevations. We also detected seasonal patterns for parasitism and natural mortality rates, sex ratio, and development time, which varied with trophic level and between elevation levels. Climate and flower abundance were important predictors for seasonal patterns in nest-building activity, ecological rates and life-history traits. These results reveal that seasonal trends in nest-building activity of lowland Hymenoptera seem to be linked to changes in climate and resource availability that reflect the seasonal patterns in plant growth and flowering documented in lowland savanna ecosystems. Higher resource availability also increased the sex ratio in bees towards the more costly females and enhanced their survival rates. These spatiotemporal links between climate, resources, ecological rates, and life-history traits indicate high sensitivity of plant-host-antagonist interactions to environmental changes.

Highlights

- Nest-building activity of cavity-nesting Hymenoptera on Mt. Kilimanjaro showed distinct seasonality at low and high elevations with concordant peaks across trophic levels.
- Ecological rates, such as parasitism or natural mortality, showed seasonality, while life-history traits more often did not.
- Seasonal patterns were more common in the colline than in the submontane zone.
- Bees, caterpillar-hunting and spider-hunting wasps showed different seasonal patterns in ecological rates and life-history traits.
- Climatic conditions and flower availability partly explained the seasonal patterns in activity of Hymenoptera, with different variables driving different rates, traits, and activity.

Keywords: antagonistic interactions, bees, elevational gradients, life-history traits, seasonal patterns, trap nests, tropical insects, wasps

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Introduction

Insect communities vary spatially and often also temporally in their abundance, diversity, and community composition. But temporal dynamics of tropical insects are poorly understood, especially along tropical elevational gradients and in the Afrotropics (Maicher et al. 2018, Maicher et al. 2019). Insects are able to survive long periods of unfavourable conditions by reducing their mortality risk in harsh seasons and finding compromises between tolerable abiotic conditions, nutritious food, and low pressure of predators, parasitoids and pathogens (Wolda 1988, Steffan-Dewenter and Schiele 2008, Abrahamczyk et al. 2011). For the purpose of survival, they have to synchronize their activity phase with suitable environmental conditions (Tauber and Tauber 1976). Abiotic factors such as temperature, humidity, and rainfall are suggested to drive these temporal variations (Frith and Frith 1990, Novotny and Basset 1998, Wagner 2001, Chen et al. 2009, Kishimoto-Yamada and Itioka 2013). However, climatic factors can only account for a fraction of seasonality in tropical communities. In the tropics, seasonal variation in climate is not as pronounced as in temperate regions. In addition, climatic conditions in the tropics are largely favourable for insects (Denlinger 1986) and in the lowland tropics neither temperature nor precipitation seem to be limiting factors. Nevertheless, there are still exceptions, such as on high mountains or during strong seasonal climatic events, like extreme dry heat or cold humidity. Furthermore, individuals have to tackle multiple trade-offs in synchronising with abiotic conditions and biotic factors, such as resource availability, while minimising intra- and interspecific competition and pressure by natural antagonists and pathogens (Denlinger 1986). Resources and antagonists also face these ecological and evolutionary challenges, which should lead to feedback loops and complex seasonal patterns. Bees, for example, can be active at lower temperatures than their parasites, so that an increase in temperature can lead to an increase in parasitism rates (Forrest and Chisholm 2017). Temporal periodicity is a basic element of ecosystems worldwide and critical to investigate in order to predict the effects of global change on species communities (Tonkin et al. 2017, Maicher et al. 2018, Maicher et al. 2019). But the degree to which tropical insects show seasonality in activity, reproduction, and traits is little understood (Maicher et al. 2019).

Seasonal changes in population size and species composition are presumably also reflected in the life-history traits of insect communities (Samnegård et al. 2015, Osorio-Canadas et al. 2018). For example, there are seasonal changes in the body size of bee communities (Osorio-Canadas et al. 2016). Larger bees need more resources for their offspring than small species (Müller et al. 2006) and therefore decline faster in abundance when resources become scarce (Bartomeus et al. 2013). Moreover, seasonal variability is also known in sex ratios (Tepedino and Parker 1988, Martins et al. 1999; for theoretical illustration, see Fig. 1). Depending on which abiotic or biotic factors drive seasonal patterns in activity, ecological rates (such as parasitism, natural mortality, and survival), and life-history traits (such as sex ratio, size, or development time), seasonal patterns are expected to differ in time and magnitude.

In addition, with the seasonal change of traits, the species community may also change functionally, because different species follow different strategies to cope with trade-offs. Moreover, drivers of seasonality can be group-specific, with some insect orders being more abundant in the dry seasons and others more abundant in the wet seasons (Wagner 2001).

For instance, bees depend on flowers as a food resource and flowering plants are largely dependent on rainfall in seasonal dry habitats. In South Africa, the occurrence of bees overlaps with seasonality in precipitation (Kuhlmann 2009). Spider-hunting wasps might not be as directly dependent on climatic seasonality as bees. Higher trophic levels should follow population dynamics of lower trophic levels, with generally lower abundances and consequently weaker amplitudes in fluctuation (Lotka 1925, Volterra 1926). Accordingly, the magnitude of seasonality may vary among taxonomic groups, showing stronger or weaker reactions to climatic seasonality, and may vary within the same group in relation to habitat type (Wagner 2001). Therefore, different seasonal patterns and different magnitudes in seasonality taken together, can be reflected in changes in the composition of the community during the year.

Since insect communities change along elevational gradients and responses of species likely vary due to different life-histories, behaviour, and interactions (Boulter et al. 2011), seasonal patterns of insect communities might also change with elevation. On the one hand, seasonal patterns along elevational gradients might change due to a turnover of species and, on the other hand, due to a change of environmental pressures (i.e., abiotic and biotic factors) with elevation. Seasonal changes in favorable conditions should directly or indirectly dictate the activity of insects (Wagner 2001). Mountains with a dry base like Mt. Kilimanjaro have a higher climatic seasonality in the lowland savannah ecosystems with aridity in the dry season and humid conditions in the rainy season than the montane forests at high elevations. Therefore, insect communities should face stronger seasonality at lower than at higher elevations on dry base tropical mountains, which might not be true for wet base tropical mountains. Also, Plant et al. 2018 found higher seasonal constraints for low-elevation assemblages for Diptera and Auchenorrhyncha. The few previous studies exploring seasonality in insect communities at different elevations did not provide consensual results on the presence (Janzen et al. 1976) or absence of an elevation effect (Boulter et al. 2011, Lambkin et al. 2011, Bishop et al. 2014, Wardhaugh et al. 2018). Therefore, there is a critical need to study how elevation, resource availability, and species interactions affect the seasonality of insect communities, especially in the tropics.

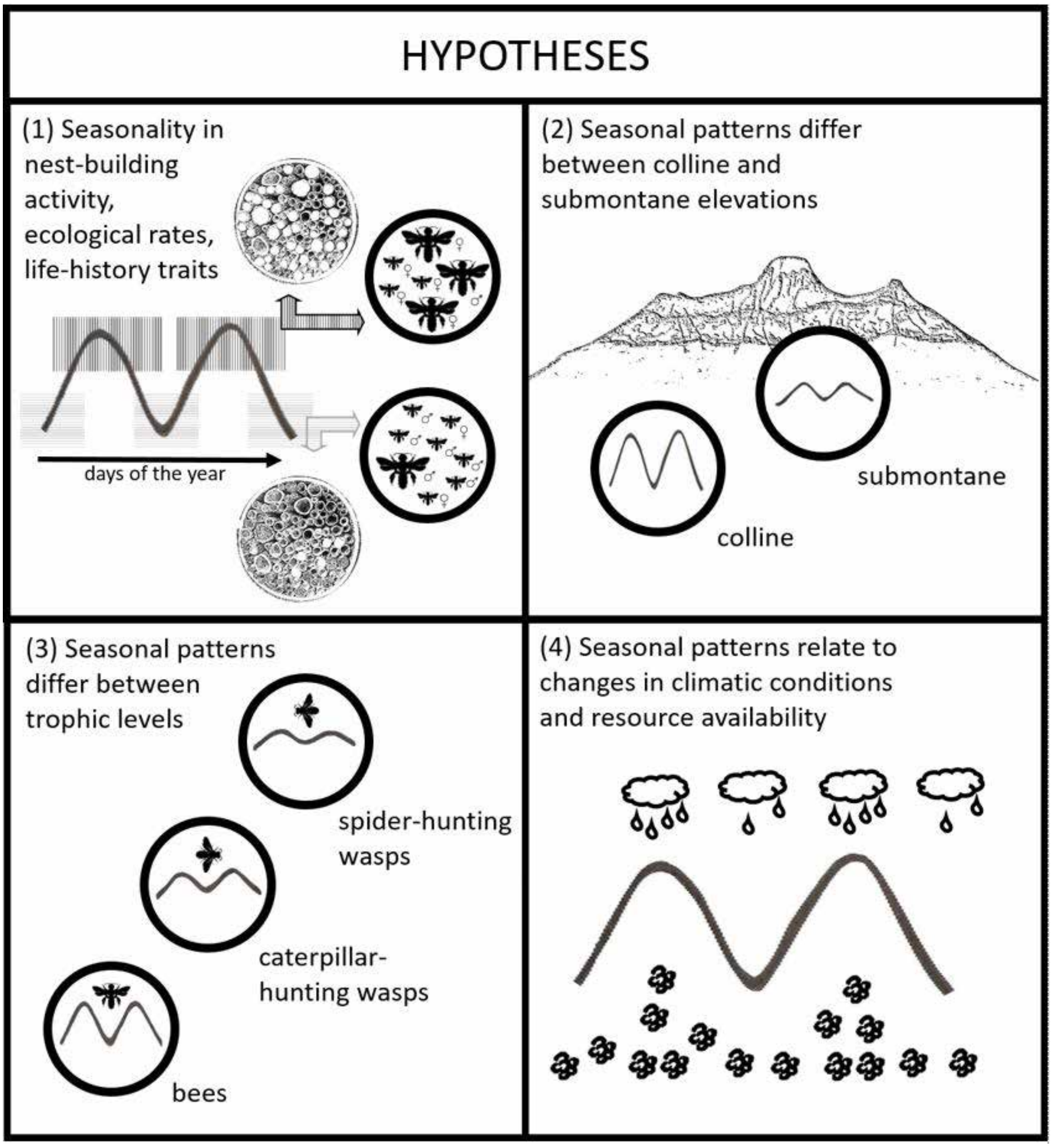

Figure 1. Illustration of proposed hypotheses. (1) The nest-building activity of cavity-nesting Hymenoptera varies seasonally. Seasonal patterns are also reflected in ecological rates (parasitism, natural mortality, and survival rate) and life-history traits (sex ratio, development time, and size). (2) The seasonal patterns differ between the colline and submontane zone. (3) The seasonal patterns differ between different trophic levels – bees, caterpillar-hunting wasps, and spider-hunting wasps – in timing and magnitude. (4) The seasonal patterns relate to changes in climatic conditions and resource availability, but the responses differ among trophic levels and elevation zones.

In order to explore different species strategies to cope with environmental trade-offs in different environments, we assessed seasonal changes in nest-building activity, ecological rates, and life-history traits of three different functional groups of cavity-nesting Hymenoptera at elevations below (colline zone: natural savannah and maize fields) and above 1,300 m a.s.l. (submontane zone: traditional agroforestry systems, extensively-used grasslands, coffee plantations) at Mt. Kilimanjaro, Tanzania. Mt. Kilimanjaro, with its dry base but wet middle elevations and a bimodal rainfall pattern over the year, provides a unique system to study seasonal patterns along an elevational gradient (Peters et al. 2019). We monitored (*i*) bees (pollinators), (*ii*) caterpillar-hunting wasps (first-order predators), and (*iii*) spider-hunting wasps (second-order predators) over a complete annual period covering two rainy and two dry seasons. We measured and analysed the number of nests, ecological rates (parasitism, natural mortality, and survival rates) and life-history traits (sex ratio, development time, and body size) for each functional group at different elevation zones. We also recorded local climatic conditions and the availability of flower resources given that cavity-nesting

Hymenoptera are sensitive to environmental changes (Tscharntke et al. 1998). We tested the following hypotheses, which are illustrated in Fig. 1:

(1) Cavity-nesting Hymenoptera show seasonality in tropical mountain ecosystems in nest-building activity, ecological rates (parasitism, natural mortality, and survival rate), and life-history traits (sex ratio, development time, and size);

(2) Seasonal patterns differ between the colline and submontane zone, with higher seasonality in the colline and lower seasonality in the submontane zone, due to stronger climatic seasonality in the colline than submontane zone at Mt. Kilimanjaro;

(3) Seasonal patterns differ between bees, caterpillar-hunting and spider-hunting wasps in timing and magnitude;

(4) Seasonality in cavity-nesting Hymenoptera is related to changes in climatic conditions and resource availability, but responses differ among elevational levels and functional groups.

Materials and Methods

Study region and study design

The study was conducted on the southern slopes of Mt. Kilimanjaro (3°10´-3°23´S, 37°14´-37°41´E) between October 2014 and February 2016. The climate is generally very dry compared to other tropical land areas and has a bimodal precipitation pattern with a long rainy season from March to May and a short rainy season between October and December (Fig. 2). A long dry season spans from June to September and a short dry season from January to February (Yang et al. 2015). Temperatures are generally higher between October and February (Appelhans et al. 2016). The climatic seasonality is much stronger in the colline zone below the forest belt (Appelhans et al. 2016). We selected 26 study sites of 50 × 50 m, ranging from 866 to 1,788 m a.s.l. (Supplementary material, Fig. S1), which we identified as the upper limit of the distribution of cavity-nesting Hymenoptera in a previous study (Mayr et al. 2020). Study sites covered five major ecosystem types found at the southern slopes of Mt. Kilimanjaro, each with five to six replicates, ranging from natural savannahs and maize fields in the colline zone, which are the driest areas of the mountain (Appelhans et al. 2016), to diverse agroforestry systems of the local Chagga tribe (Chagga homegardens), extensively-managed grasslands and coffee plantations in the submontane zone. One study site had to be excluded because we recorded no nests. For statistic robustness of seasonal trends (i.e., to ensure a sufficient amount of data at each elevation), we divided study sites into two elevational levels, colline zone (<1,300 m a.s.l., i.e. 866-1,275 m a.s.l., N = 13 study sites) and submontane zone (≥1,300m a.s.l., i.e. 1,303-1,788 m a.s.l., N = 12 study sites).

Sampling of cavity-nesting Hymenoptera

The seasonal abundance of cavity-nesting bees, crabronid, eumenid, pompilid, and sphecid wasps (Fig. 3d) and their natural antagonists (Fig. 3e) was assessed with 208 trap nests operated for 17 months. Cavity-nesting Hymenoptera fulfill important ecosystem

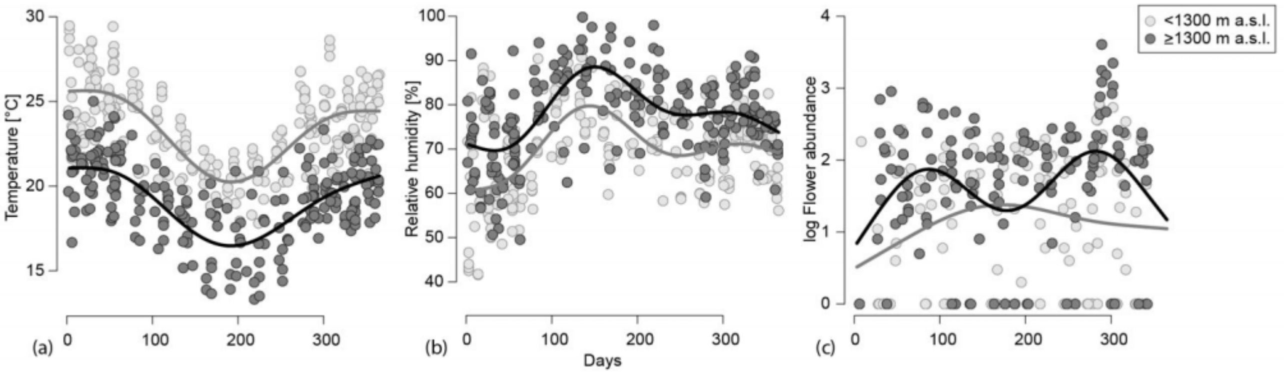

Figure 2. Seasonal variation of temperature, relative humidity, and flower abundance at elevations below (colline) and above 1,300 m a.s.l. (submontane zone) at Mt. Kilimanjaro. Generalized additive mixed models (GAMM) were used to estimate trends of seasonality (Gaussian family, basis dimension (k) = 6 as for nest-building activity, life-history traits, and ecological rates. Temperature, relative humidity, and flower abundance (log-transformed) showed significant seasonality in the colline and submontane zone. Colline zone: (a) Temperature: $F_{5,735}$=309, p<0.001, (b) Relative humidity: $F_{5,735}$=84.79, p<0.001, (c) Flower abundance: $F_{3,443}$=7.31, p<0.001. Submontane zone: (a) Temperature: $F_{5,678}$=286.6, p<0.001, (b) Relative humidity: $F_{5,678}$=90.72, p<0.001, (c) Flower abundance: $F_{5,432}$=13.2, p<0.001. Trend lines derived with GAMMs were plotted with continuous lines because the significance level of days of the year was p < 0.05 and a seasonal pattern was observed. A linear mixed effect model (LMM) with study site as random factor was used to test for possible correlations between temperature and humidity and flower abundance. Flower abundance correlated with temperature (t-value=-3.14, p<0.01), relative humidity (t-value=1.79, p=0.07) and an interaction of both temperature*relative humidity (t-value=8.33, p<0.001). Days: Days of the year.

Figure 3. Trap nests for cavity-nesting Hymenoptera. (a) Trap nests at ground level being approached by probably a *Megachile (Pseudomegachile) sinuata* (Friese) bee. (b), (c) Trap nests at canopy level. (d) *Megachile sp.* providing a brood cell with pollen, and (e) cuckoo bee *Euaspis abdominalis* opening a host nest. (f) Opened *Nothylaeus* nest with pupae in the first brood cell and following dead brood cells for unknown reason.

functions like pollination and predation (Losey and Vaughan 2006). These groups lay eggs in cavities which the sampling with trap nests aims to mimic. Eight trap nests were placed in four pairs on each study site and filled with common reed (*Phragmites australis*) and Japanese knotweed (*Fallopica japonica*) internodes (Fig. 3a-c). On study sites with trees, such as savannah, Chagga homegardens, and coffee plantations, two pairs were placed at canopy level and two pairs at ground level. On study sites without trees, like maize fields and grasslands, the four pairs were placed at ground level. Each trap nest consisted of ~120 internodes, ranging from 2-25 mm diameter to offer cavities for small and large species. The trap nests were checked monthly for new and hatched nests, and occupied reed internodes were replaced with new ones. We reared all nests in hatching boxes on the study sites in order not to change the climatic conditions during development. After hatching, all nests were cut open (Fig. 3f), morphospecies were identified, and nest-building activity, ecological rates and life-history traits were recorded. For more information and pictures about the trap-nesting method see Mayr et al. 2020. The nest-building activity was used as a proxy for the reproduction activity. Chosen ecological rates and life-history traits are described below. All specimens were divided into functional groups following the trophic level of their food provisions, i.e., pollen and nectar feeders (bees: Apidae), caterpillar-hunting wasps (Eumeninae), and spider-hunting wasps (Pompilidae, Sphecidae and Crabronidae). Aphid-hunting, cicada-hunting, and orthopteran-hunting wasps occurred only occasionally so that we excluded them from the analysis.

Measurement of ecological rates and life-history traits

We measured ecological rates (1)-(3), life-history traits (4)-(6) from nests and specimens for each trophic level, and the colline and submontane zone (Table 1): (1) we calculated the mean parasitism rate as the number of brood cells killed by parasitoids, predators, and cleptoparasites divided by all brood cells, i.e., all cells that were occupied. We also used the number of brood cells killed by parasitoids, predators and cleptoparasites directly. (2) We determined the mean natural mortality as the number of dead brood cells that died for unknown reason (presumably pathogens)

Table 1. Summary of the seasonal patterns investigated in nest-building activity, ecological rates, and life-history traits of bees, caterpillar-hunting, and spider-hunting wasps in the colline and submontane zone of Mt. Kilimanjaro.

			Ecological rates			Life-history traits		
Hym. group	**Elevational level**	**Nest-building activity**	**Parasitism rate**	**Natural mortality rate**	**Survival rate**	**Sex ratio**	**Development time**	**Size**
Bees	colline	▨ ✓		▨ ✓	▨ ✓	▨ ✓		
Bees	submontane	✓		▨ ✓	▨ ✓			
Wlep	colline	▨ ✓	▨ ✓	✓	✓		▨ ✓	
Wlep	submontane	✓	✓					
Wara	colline	▨ ✓	✓	▨ ✓	▨ ✓		▨ ✓	
Wara	submontane	✓	▨ ✓		▨ ✓			✓

Significant seasonal patterns are ticked. Seasonal patterns which correlated with temperature, relative humidity, an interaction of both, or flower abundance are shaded dark grey. Hym. group: Hymenoptera group, Wlep: caterpillar-hunting wasps, Wara: spider-hunting wasps.

divided by all brood cells. Potential problems with the natural mortality may occur when parasitised brood cells would have died for unknown reasons anyway. In these cases, the actual natural mortality would be higher. However, there is evidence that hymenopteran predators, such as ants, are able to sense and avoid infected prey (Pereira and Detrain 2020). To avoid prey of lower quality, parasitoids might be able to sense infected hosts as well. Nevertheless, a potential bias by parasitism should be kept in mind. (3) The mean survival rate was calculated as the number of hatched brood cells divided by all brood cells. (4) We calculated the mean sex ratio as the number of male brood cells divided by all brood cells. (5) We measured the mean development time as the number of days between the date of control when the nests were found and the date of control when the nests were already hatched. This implies that the real development time can differ from the measured development time. It can be longer if nests had been built already 1-4 weeks before the control date and shorter if nests had already hatched 1-4 weeks before the control date. The development time is therefore a coarse estimate to differentiate very short and very long development times. (6) Lastly, we measured the diameters of occupied reed internodes, which correlate with body size with few exceptions (Araújo et al. 2016), to estimate mean body size of the community. Sample size may differ among life history traits, as some traits are mutually exclusive. For example, sex cannot be determined for an individual killed by a parasitoid.

Temperature, relative humidity and flower abundance

Temperature and relative humidity were recorded in 5-minutes intervals during the whole duration of the data collection (Appelhans et al. 2016) and averaged to daily means. We used a co-kriging approach to estimate missing temperature and humidity values for two study sites, where data loggers were not running during the whole duration of the data assessment (Appelhans et al. 2016). Data for flower abundance of flowering plant species were collected in parallel to the trap-nest surveys each month along two parallel 50 m transects of 2 m width and a distance of 20 m to each other, and the total number of flowers per species was assessed for each survey. Compound flowers were considered as a unit for flower distances which a small bee of approx. 1 cm length would rather walk than fly (Classen et al. 2015).

Statistical analysis

All statistical analyses were performed using the R Project for Statistical Computing version 3.3.3 (R Development Core Team 2018). The seasonal pattern of nest-building activities, ecological rates, and life-history traits were modelled as a function of the day of year using generalized additive mixed models (GAMMs) with a Gaussian error structure, Poisson error structure, or Binomial error structure depending on the variable considered (*gamm* function in the *mgcv* R-package). Nest-building activities were modelled with Poisson error structure, while size and development time were modelled with Gaussian error structure. Sex ratio, parasitism, natural mortality, and survival rate were modelled with Binomial error structure with logit link function. GAMMs are modelling techniques that allow temporal spline fitting while taking account of repeated measurements on statistical units. Herein, the identities of the site were specified as a random variable. For statistical robustness of seasonal trends (i.e., to ensure a sufficient amount of data at each time period), time was rescaled on Julian dates from the first of January to show a complete annual cycle. We performed models for study sites <1,300 m and ≥1,300 m a.s.l. and for each functional insect group separately as the inference and interpretation of statistical interactions between predictor variables is rather complicated with GAMMs. In GAMM models we set the basis dimension of the smoothing term *k* to six to account for seasonal patterns in the trend functions while limiting the complexity of the curve function. To account for some losses of nests out of the hatching boxes (due to destruction or theft by humans), we estimated the number of established nests for each functional group by multiplying the total number of primarily observed nests with the proportion for each functional group observed in the remaining nests. Because losses were random, we assumed that the relative proportion of functional groups did not change with some nests lost. In total, 13% of the primarily observed nests were lost.

We tested whether the seasonality in nest-building activity, ecological rates, and life-history traits is synchronised with temperature, relative humidity, an interaction of both, and the abundance of flowers using generalised linear mixed effect models (GLMMs, *glmer* function in the *lme4* R-package) following the same error structures as described for the GAMMs. Site was specified as a random variable in models to account for repeated measurements on the same study site. We calculated all models first with data points covering the whole elevational gradient to reveal general seasonal patterns and then recalculated the models for the colline and submontane zone separately to check for causalities which might only occur within a certain elevational level. Before the analyses, the explanatory variables were standardized by z-transformation using the *scale* function in R. We further checked whether seasonal patterns in nest-building activity between functional groups are synchronised between each other using linear mixed effect models (LMMs, *lmer* function in the *lme4* R-package) with study site as random factor to correlate nest-building activities of different functional groups.

In order to check turnover of species communities between seasons and elevations, we used a subset of nests in which the host could be identified to morphospecies level. We calculated a non-metric multidimensional scaling (NMDS) based on Bray-Curtis distances between species occurrences (species present or absent) of colline (<1,300 m a.s.l.) and submontane elevations (≥1,300 m a.s.l.) and four different seasons (long rainy season: March-May; long dry season: June-September; short rainy season: October-December and short dry season: January-February), using the *metaMDS* function in the *vegan* R-package and a community matrix with occurrence data.

Results

The highest number of flowers were recorded in October both in the colline and submontane zone and positively correlated with relative humidity (Fig. 2). In total, we dissected 6,852 nests of cavity-nesting Hymenoptera, of which 5,973 could be identified in detail for life-history traits and ecological rates and 87% of them could be assigned to bees, caterpillar-hunting wasps, and spider-hunting wasps. Altogether, we were able to identify 2,230 nests at species level, which comprises 33% of all observed nests, belonging to 88 host morphospecies (Supplementary material, Table S3). Overall, bees built the highest numbers of nests (54% of all identified nests), followed by caterpillar-hunting wasps (20%), and then spider-hunting wasps (14%). We found seasonal patterns in nest-building activity, ecological rates, and life-history traits, presented in detail below, which differed between trophic levels and between the colline and submontane zone (Table 1). The results are presented in a graphical summary to facilitate the link to the hypotheses (Fig. 4).

Seasonal patterns in nest-building activity and species turnover

Nest-building activity varied seasonally in the colline and submontane zone (Fig. 5). All three functional groups showed seasonality in nest-building activities in the colline and submontane zone, with strongest seasonality in the colline zone (Fig. 5; Supplementary material, Fig. S4). Strikingly, seasonal patterns in nest-building activity were similar between all functional groups in the colline zone, with a peak in the transition between short rainy and short dry season. In the submontane zone seasonal patterns were only similar for caterpillar- and spider-hunting wasps, with a peak in the transition between short dry and long rainy season (Fig. 5).

The seasonal turnover in species communities seemed to be generally low, with slightly lower turnover observed in the colline than in the submontane zone (colline: mean distance to centroid = 0.25; submontane: mean distance to centroid = 0.28). Elevational turnover was high, forming generally very distinct species communities between elevation zones (Supplementary material, Fig. S2). Seasonal overlap in species composition between the two studied elevational zones of Mt. Kilimanjaro was also low, i.e., species which were found in the colline zone during one season did not occur in the submontane zone during another season and vice versa.

Seasonal patterns in ecological rates

Overall, we observed strong seasonal variations in natural mortality, parasitism, and survival rates with strong variations depending on functional group and elevation (Fig. 6; Supplementary material, Fig. S3, Fig. S4). Natural mortality rate of bees and caterpillar-hunting wasps increased at the end of the warm rainy season in the colline zone (Fig. 6; Supplementary material, Fig. S4). It then decreased again at the end of the warm dry season in the colline zone (Fig. 6; Supplementary material, Fig. S4). The natural mortality rate of bees showed opposite trends in the submontane zone (Fig. 6; Supplementary material, Fig. S4). In contrast, the parasitism rate of caterpillar-hunting wasps peaked in the colline zone in the transition time between short dry and long rainy and again between long dry and short rainy season (Fig. 6; Supplementary material, Fig. S4), but the highest number of parasitized brood cells were found in the transition times between rainy and dry seasons (Supplementary material, Fig. S5). In opposition to the caterpillar-hunting wasps, the parasitism rate of the spider-hunting wasps peaked in the transition time between long rainy and long dry season, with highest numbers of parasitized brood cells in the rainy seasons, and the parasitism rate was similar in the colline and submontane zone, with lower parasitism rates at the beginning and end of the year (Fig. 6; Supplementary material, Fig. S4, Fig. S5). The survival rate of bees showed opposite patterns to the natural mortality rate of bees (Supplementary material, Fig. S4). In the colline zone, the survival rate of bees peaked twice, in the long dry season and towards the short rainy season. The survival rate of caterpillar-hunting wasps peaked with the first peak of bees and the survival rate of spider-hunting wasps with the second peak of bees in the colline zone (Supplementary material, Fig. S3).

Seasonal patterns in life-history traits

We found only few significant seasonal trends for variation in sex ratio, development time, and size (Fig. 7, Table 2; Supplementary material, Fig. S3, Fig. S4, Table S1). For bees in the colline zone, the sex ratio increased towards more males in the transition

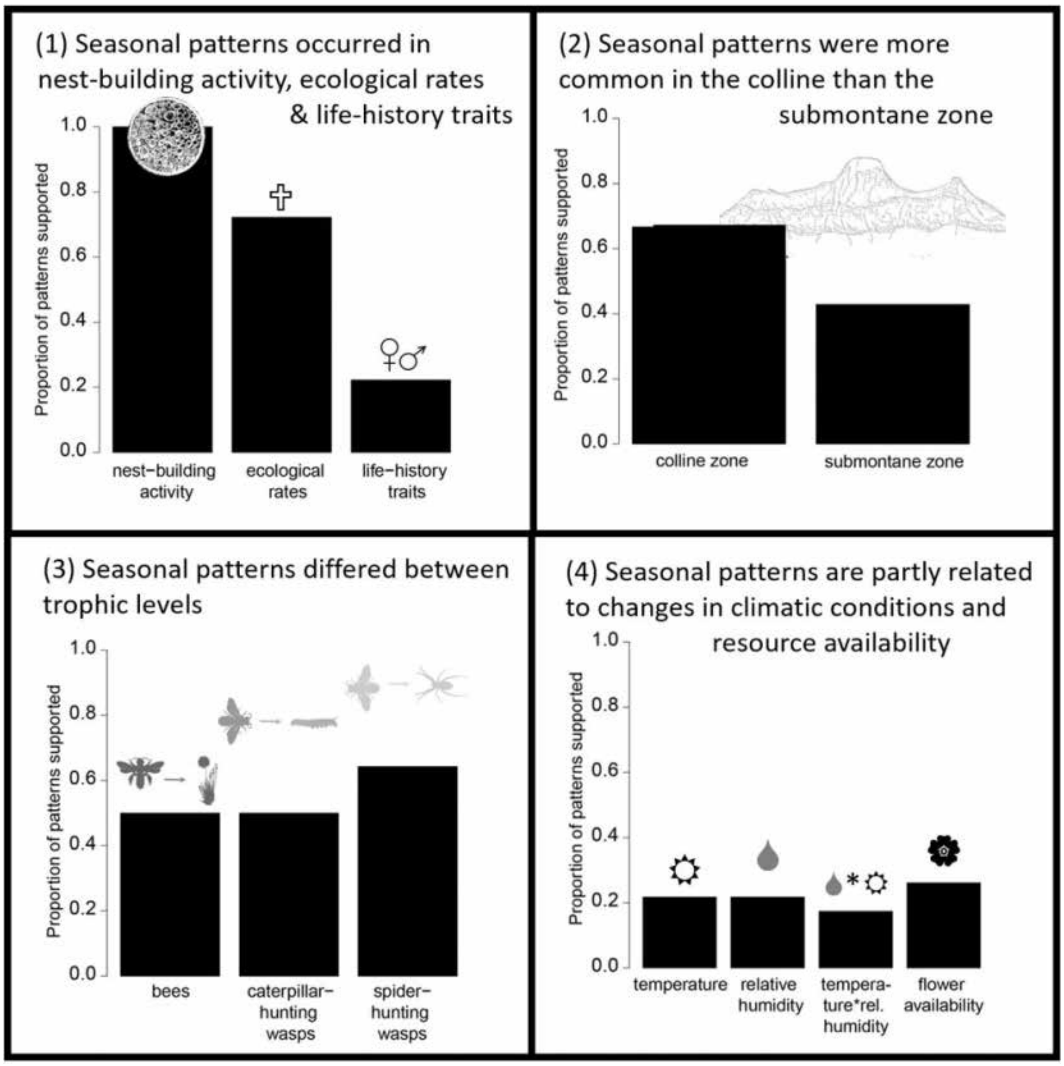

Figure 4. Overview of the results according to the hypothesis. (1) Seasonal patterns occurred in nest-building activity, ecological rates, and life-history traits. Seasonal patterns were most common in the nest-building activity (they occurred in all trophic levels and in both elevation zones – three trophic levels times two elevation zones). They were not present for all trophic levels and elevation zones in ecological rates (only 13 seasonal patterns out of 18 possible seasonal patterns - three trophic levels times two elevation zones times three ecological rates). They were least common in life-history traits (only four seasonal patterns out of 18 possible seasonal patterns). (2) The seasonal patterns differed between the colline and submontane zone for most traits. In the colline zone, more traits showed seasonal patterns (14 seasonal patterns out of 21 possible ones – seven traits times three trophic levels). (3) The seasonal patterns differed between trophic levels in timing and magnitude for most investigated traits. Spider-hunting wasps showed most seasonal patterns in traits (nine seasonal patterns out of 14 possible ones – seven traits times two elevation zones), caterpillar-hunting wasps and bees were equal. (4) Seasonal patterns were partly related to seasonal changes in climatic conditions and resource availability. Out of 23 observed seasonal patterns, six were correlated with flower abundance, five with temperature or relative humidity, and four with an interaction of both temperature and relative humidity. For some seasonal patterns, more than one driver was found.

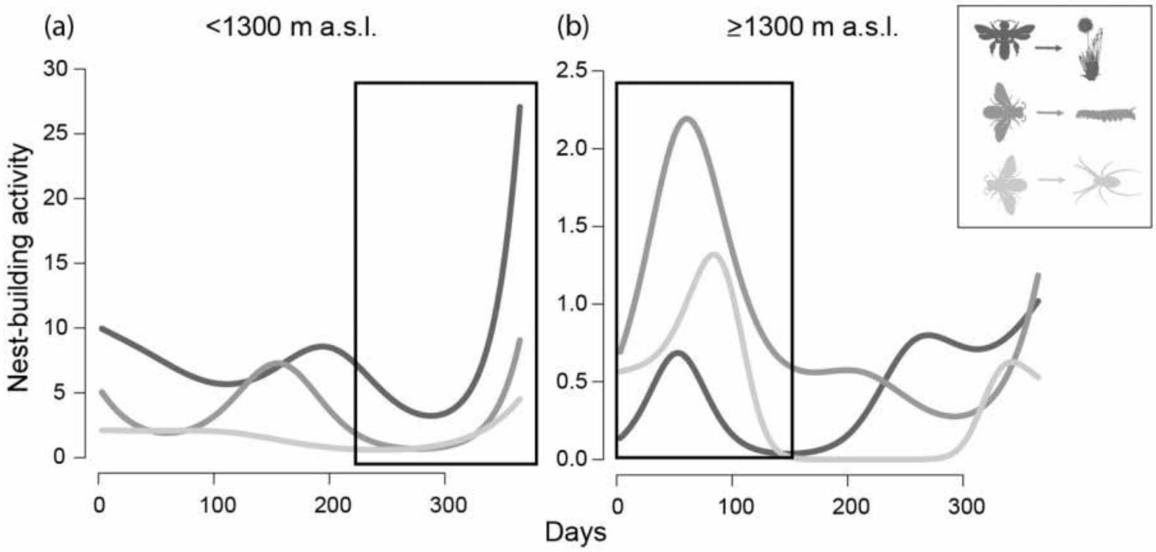

Figure 5. Seasonal variation of nest-building activities of bees, caterpillar-hunting wasps (Wlep) and spider-hunting wasps (Wara) at elevations (a) below and (b) above 1,300 m a.s.l. at Mt. Kilimanjaro. Generalized additive mixed models (GAMM) were used to estimate trends of seasonality (Poisson family, basis dimension (k) = 6. Nest-building activities of bees, Wlep and Wara showed significant seasonality in the colline and submontane zone: Colline zone: Bees: $F_{5,206}$=137.8, p<0.001, Wlep: $F_{5,206}$=74.64, p<0.001, Wara: $F_{5,206}$=33.78, p<0.001, submontane zone: Bees: $F_{5,183}$=37.12, p<0.001, Wlep: $F_{5,183}$=25.91, p<0.001, Wara: $F_{5,183}$=10.89, p<0.001. Seasonal synchrony in nest-building activities was tested with linear mixed effect models (LME). The nest-building activity of bees, Wlep and Wara were similar in the colline zone, but in the submontane zone only for Wlep and Wara: Colline zone: Bees-Wlep: t=1.97, p=0.05, Bees-Wara: t=4.66, p<0.001, Wlep-Wara: t=5.48, p<0.001, submontane zone: Bees-Wlep: t=-0.21, p=0.84, Bees-Wara: t=0.91, p=0.37, Wlep-Wara: t=2.10, p=0.04. Bees, caterpillar-hunting and spider-hunting wasps showed synchronised seasonality at the end of the year in the colline zone, but they were rather synchronised at the beginning of the year in the submontane zone, illustrated by the black frames. Only model predictions are displayed because nest-building activity contains extreme values. Only GAMM predictions are shown for clarity, but see Fig. S3.2 for observed data Days: Days of the year.

between warm rainy and warm dry season (Fig. 7; Supplementary material, Fig. S4(a)). The development time for caterpillar- and spider-hunting wasps slightly increased during the long rainy season in the colline zone. In general, the mean size of cavity-nesting Hymenoptera was rather similar throughout the year with only the spider-hunting wasps in the submontane zone showing seasonal trends in body size, i.e., a larger size in the warmer half of the year (Supplementary material, Fig. S3(b), Fig. S4(c)).

Drivers of seasonal patterns

We observed for 15 seasonal patterns in nest-building activity, ecological rates or life-history traits (out of 23 seasonal patterns in total), correlations with climate, and/or flower availability (Table 1). The explanatory variables differed partly with variable, trophic level, and elevation zone (Table 2, Supplementary material, Table S2).

Nest-building activity of bees increased with flower abundance, whereas nest-building activity of spider-hunting wasps increased with temperature and relative humidity, and in caterpillar-hunting wasps higher nest numbers were explained by an interaction of temperature and relative humidity (Table 2).

The parasitism rate increased for caterpillar-hunting wasps with increasing temperature in the colline zone. The parasitism rate increased for spider-hunting wasps with increasing temperature in the submontane zone but only, if the relative humidity was below 70%, and it decreased with temperature if the relative humidity was above 70% (Supplementary material, Table S2). Natural mortality rate of bees and caterpillar-hunting wasps increased with relative humidity and decreased for bees with increasing temperature in the colline zone (Table 2; Supplementary material, Fig. S4). The survival rate of bees increased with temperature and flower abundance. The survival rate of caterpillar-hunting wasps was also enhanced by flower abundance, but decreased with relative humidity. The survival rate of spider-hunting wasps was explained by an interaction between temperature and relative humidity, i.e., higher temperature in concert with low relative humidity lead to higher survival rates (Table 2).

A lower flower abundance lead to a higher proportion of bee males in the colline zone (Supplementary material, Table S2). The development time of caterpillar- and spider-hunting wasps positively correlated with relative humidity, and for spider-hunting wasps it was also correlated with temperature in the colline zone (Supplementary material, Table S2).

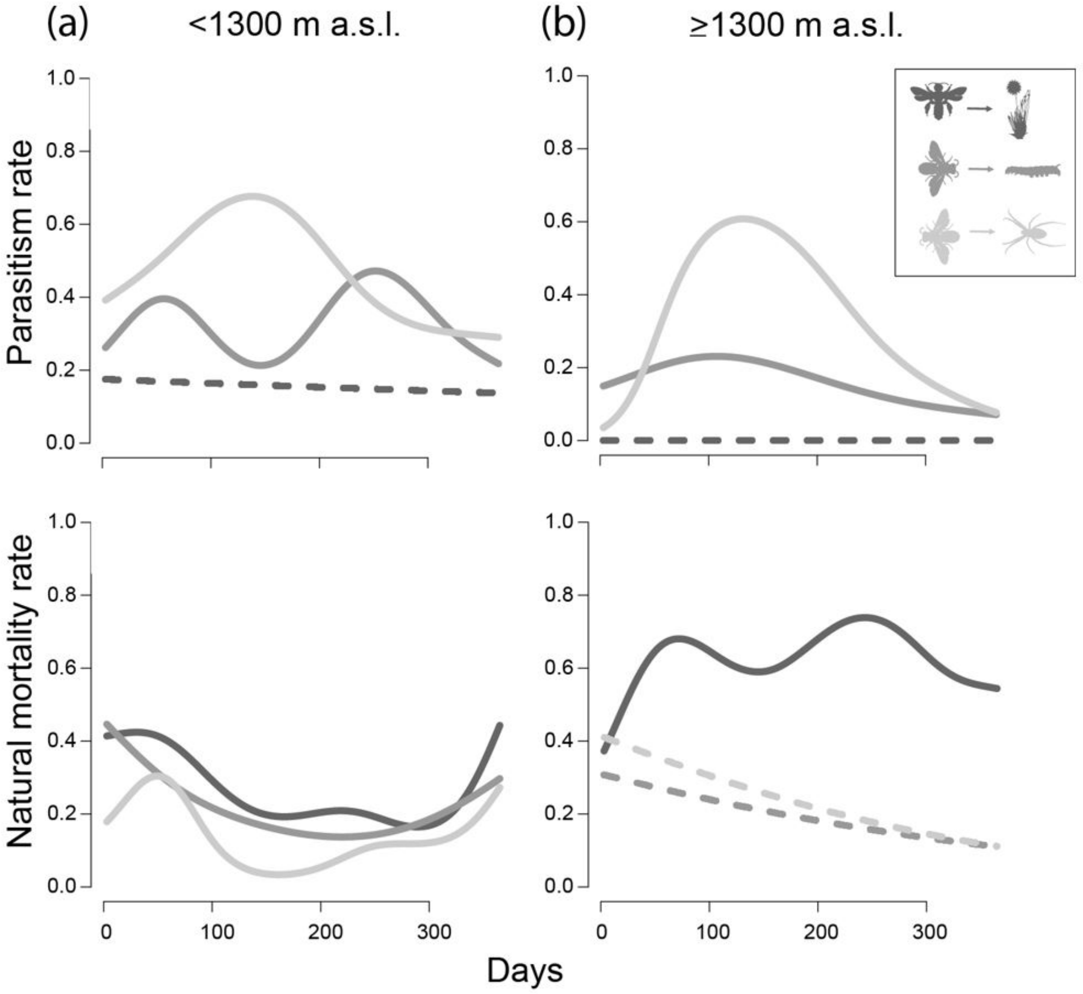

Figure 6. Seasonal variation in ecological rates. Shown are parasitism and natural mortality rates of bees, caterpillar-hunting wasps, and spider-hunting wasps at elevations (a) below and (b) above 1,300 m a.s.l. at Mt. Kilimanjaro. Generalized additive mixed models (GAMM) were used to estimate trends of seasonality (Binomial family for parasitism and natural mortality rate, basis dimension (k) = 6). Significant model GAMM estimations are shown with solid lines, not significant model estimations with dashed lines. Model statistics are given in Table S3. Only GAMM predictions are shown for clarity, but see Fig. S3.2 for observed data Days: Days of the year.

No correlation was found between size and climate nor between size and flower availability.

Discussion

We investigated seasonal patterns of nest-building activities, species turnover, ecological rates, and life-history traits for three different functional groups of cavity-nesting Hymenoptera in the colline and submontane zone in a tropical mountain ecosystem. Consistent with hypothesis 1, we found that seasonal patterns in nest-building activity were also reflected in seasonal variation of parasitism and natural mortality rate, sex ratios, development time, and body size. Seasonal patterns occurred in the colline and submontane zone and in all investigated groups, i.e., bees, caterpillar-hunting wasps and spider-hunting wasps but differed between the colline and submontane zone (hypothesis 2) and between groups (hypothesis 3). Our data indicate that seasonal patterns are often driven by environmental factors (hypothesis 4) –temperature, relative humidity, an interaction of both variables, and also flower abundance, in the case of bees. By demonstrating seasonal patterns in different ecological rates and life-history traits, at different elevations and in different functional groups, our study provides new insights about the community composition and biotic interactions of tropical insects under changing environmental conditions. Furthermore, it is the first study that provides seasonal patterns in cavity-nesting hymenopterans with simultaneous comparison at different elevations. Previously, seasonal patterns in cavity-nesting hymenopterans have mainly been investigated in temperate regions (Tylianakis et al. 2005, Matos et al. 2016, Sabino and Antonini 2017)

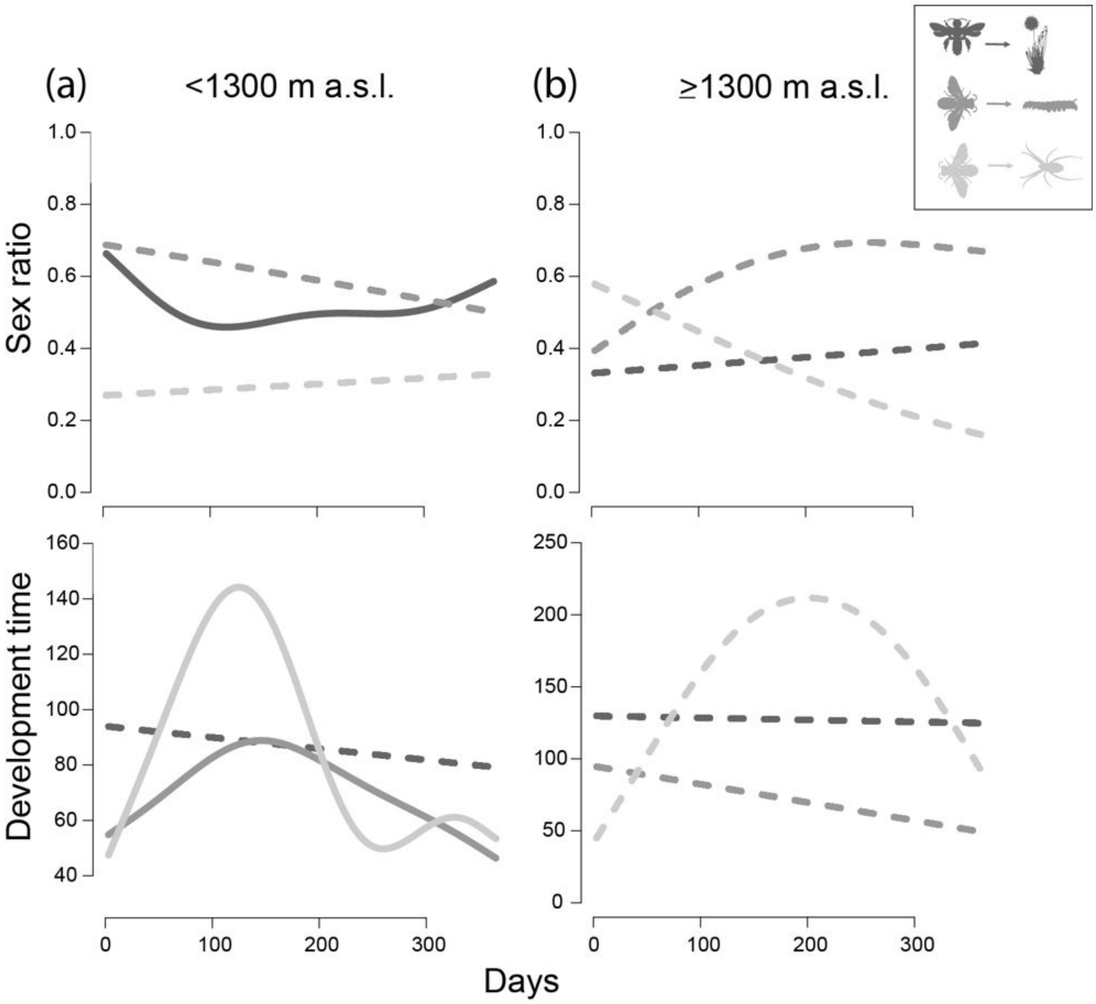

Figure 7. Seasonal variation in life-history traits. Shown are sex ratio and development time of bees, caterpillar-hunting wasps, and spider-hunting wasps at elevations (a) below and (b) above 1,300 m a.s.l. at Mt. Kilimanjaro. Generalized additive mixed models (GAMM) were used to estimate trends of seasonality (Binomial family for sex ratio, Gaussian family for development time, basis dimension (k) = 6). Significant model GAMM estimations are shown with solid lines, not significant model estimations with dashed lines. Model statistics are given in Table S3. Only GAMM predictions are shown for clarity, but see Fig. S3.2 for observed data Days: Days of the year.

at similar elevations and with less detail with regard to groups, ecological rates, and life-history traits.

Synchronised nesting-activity between bees and wasps in the colline zone

In line with hypothesis 3, the magnitude of seasonality in nest-building activity differed between functional groups, but in contrast to our assumption, it was synchronised in the colline zone with a strong peak at the end of the short rainy season for bees, caterpillar- and spider-hunting wasps. Seasonal patterns are believed to differ between species, families or other taxonomic groups (Wolda and Roubik 1986, Sirohi et al. 2015, Osorio-Canadas et al. 2018), but except for small differences, we rather found differences in magnitude than in seasonal timing of activity. A similar tendency was found in a leaf-roller community and herbivores seemed to fluctuate higher with seasonality than the predators (Vieira and Romero 2013). In the submontane zone, with much lower nest densities, nesting activity was less synchronised and generally less subject to strong fluctuations, confirming hypothesis 2.

The period of nesting is the most critical life stage for solitary insects, because unlike social species, females spend most of their time constructing and provisioning their nests (Morato and Martins 2006). Therefore, it must be carefully adapted to seasonal variation in abiotic and biotic environmental conditions. Warmer temperatures and the start of the short rainy season in October seemed to trigger different insect groups in the colline zone and synchronise their life-cycles. Most insect species in the tropics peak in the rainy season or in the transition time between rainy and dry season (Frith and Frith 1990, Novotny and Basset

Table 2. Summary of the GLMM models performed to test the effects of temperature, relative humidity, flower abundance, and an interaction between temperature and relative humidity on seasonal patterns of nest-building activity, ecological rates, and life-history traits.

Variable	Hym. group	T		rH		T*rH		Flower ab.	
		t/z-value	p-value	t/z-value	p-value	t/z-value	p-value	t/z-value	p-value
Nest-building activity	Bees	t=0.45	p=0.65	t=-0.32	p=0.75	t=0.81	p=0.42	t=1.95	p=0.05
	Wlep	t=-0.74	p=0.46	t=-1.38	p=0.17	t=1.87	p=0.06	t=-0.31	p=0.76
	Wara	t=2.86	p<0.01	t=1.84	p=0.07	t=1.26	p=0.21	t=0.28	p=0.78
Parasitism rate	Wlep	z=-1.28	p=0.20	z=0.64	p=0.52	z=0.35	p=0.73	z=-1.56	p=0.12
	Wara	z=1.39	p=0.17	z=1.22	p=0.22	z=-0.35	p=0.73	z=-0.50	p=0.62
Natural mortality rate	Bees	z=-2.67	p<0.01	z=2.19	p=0.03	z=-0.74	p=0.46	z=1.03	p=0.30
	Wlep	z=1.10	p=0.27	z=2.40	p=0.02	z=-1.58	p=0.11	z=-1.05	p=0.29
	Wara	z=-0.26	p=0.79	z=-0.71	p=0.48	z=-2.10	p=0.04	z=-1.60	p=0.11
Survival rate	Bees	z=2.87	p<0.01	z=-1.61	p=0.11	z=-0.72	p=0.47	z=2.90	p<0.01
	Wlep	z=0.68	p=0.50	z=-2.28	p=0.02	z=1.00	p=0.32	z=2.42	p=0.02
	Wara	z=-0.93	p=0.35	z=-0.82	p=0.41	z=2.62	p<0.01	z=1.44	p=0.15
Sex ratio	Bees	z=-0.20	p=0.84	z=-0.08	p=0.94	z=-0.82	p=0.41	z=-1.74	p=0.08
Development time	Wlep	t=0.41	p=0.68	t=1.41	p=0.16	t=1.14	p=0.26	t=0.87	p=0.39
	Wara	t=0.13	p=0.90	t=0.91	p=0.37	t=0.14	p=0.89	t=1.18	p=0.25
Size	Wara	t=1.05	p=0.30	t=0.57	p=0.57	t=0.71	p=0.48	t=-0.82	p=0.42

Significant positive and negative correlations between nest-building activity and explanatory variables can be concluded from positive (blue) and negative (red) t-values, respectively. The darker the colour, the more significant the correlation. Some groups are missing for some variables in this table if they did not show a seasonal pattern. Hym. group: Hymenoptera group, T: Temperature, rH: relative Humidity, T×rH: Interaction between Temperature and relative Humidity, Flower ab.; Flower abundance, Wlep: caterpillar-hunting wasps, Wara: spider-hunting wasps.

1998, Tidon 2006, da Silva et al. 2011). However in the submontane zone, life-cycles seemed to be delayed as activity peaked in the transition time (short dry season) before the start of the long rainy season. This period, with still high temperatures and rising air humidity, seems to enable nesting by all investigated insect groups before the nest-building activity drops with the long rainy season, a period with high mean humidity between 80 and 100%. However, we observed the lowest nesting-activity during the long dry season, which is colder than the short dry season (Yang et al. 2015). During this period, the environmental conditions seem to be fundamentally hostile to all cavity-nesting Hymenoptera. Decreasing abundances of different groups of flies, which are generally able to persist under extreme climate conditions, have also been observed in the coldest and driest months (Lambkin et al. 2011).

According to hypothesis 4, environmental drivers were related to seasonality in nest-building activity, even though we found that different drivers were responsible for similar, but still slightly different, seasonal nest-building activities in the different functional hymenopteran groups. The abundance of flowering plants, which was closely linked to relative humidity in the colline zone, was the strongest trigger for the nest-building activity of bees. Many studies show that the spatial variation in floral resource abundance and diversity is related to bee diversity, but the linkage between the seasonal dynamics of flower resources and bees has been rarely achieved (e.g., Abrahamczyk et al. 2011). By analysing the colline and submontane zone separately, we found that the nest-building activity of bees was linked to flower abundance in the colline, but less so in the submontane zone. This may indicate that bees are more adapted to the onset of the rainy season in the colline than in the submontane zone. Temperature, which has been shown to be one of the most important factors for driving species diversity patterns of multiple taxa at Mt. Kilimanjaro (Peters et al. 2016), but also for cavity-nesting Hymenoptera (Mayr et al. 2020), was positively correlated with the nest-building activity of spider-hunting wasps, while relative humidity decreased it. Spider abundances at Mt. Kilimanjaro were found to be positively correlated with temperature (Röder et al. 2017) and might therefore offer high resource abundance for their predators in habitats with higher temperatures. Indeed, high temperatures correlated with a high number of nests in *Trypoxylon*, a genus of spider-hunting wasps (Loyola and Martins 2006). The nest-building activity of caterpillar-hunting wasps only increased when temperature and relative humidity were high but decreased when temperature was high and relative humidity was below 75%. This decrease of nesting-activity with high temperature and low relative humidity is prominent in the colline zone. Excessively high temperatures, especially together with low relative humidity in the colline zone might have a direct, negative impact on caterpillar abundance. This may result from caterpillars being poorly protected from excessively high temperatures due to their relatively soft cuticle. Another explanation might be that because the abundance of predators, like ants and spiders, increases with temperature (Kaspari et al. 2000, Röder et al. 2017), the abundance of their prey, such as caterpillars, might decrease, causing decreasing nest-building activities of caterpillar-hunting wasps due to lower resource availability. On the other hand, nest-building activity of caterpillar-hunting wasps was also low with relatively high humidity and low temperatures. Even though caterpillars prefer wet conditions, foraging of caterpillar-hunting wasps might be restricted when temperatures are too cold (temperature-mediated resource exploitation hypothesis; Classen et al. 2015). Overall, we assume that in both wasp groups temperature indirectly influences nest-building activity in the colline zone by temporarily limiting the availability of their resources. However, we did not observe a multi-year pattern and therefore our results have to be considered with caution.

Seasonality in ecological rates

We also found seasonal patterns for ecological rates but in line with hypotheses 2 and 3, with strong variation among elevational belts and functional groups. The parasitism rate of the caterpillar-hunting wasps in the colline zone peaked in the transition times between dry and rainy seasons and was time-delayed to the nest-building activity of the caterpillar-hunting wasps in the colline and submontane zone. Parasitoids are often well synchronised to their hosts (Martins et al. 1999, Sabino and Antonini 2017) and are often host density-dependent (Gazola and Garófalo 2009, Mesquita and Augusto 2011, Araújo et al. 2016). In our study, the number of parasitised brood cells followed the seasonal pattern of the nest-building activity of the hosts, with the highest number of parasitised brood cells at the beginning, middle, and end of the year. But increased parasitism rates may be also correlated with decreasing host abundances (Elekcioglu and Uygun 2013). The nest-building activity of caterpillar-hunting wasps in the colline zone dropped stronger and increased faster than the parasitism, and therefore the parasitism rate showed a time-delayed pattern in relation to the nest-building activity of the host.

Parasitism rates in spider-hunting wasps were similar in the colline and submontane zone, the only pattern and group contradicting hypothesis 2. No spider-hunting nests occurred in the middle of the year. While we observed that the nest-building activity of spider-hunting wasps decreased towards the middle of the year, showing a similar pattern for the colline and submontane zone, the number or parasitised cells did not drop as strong as the nest-building activity of the hosts so that the parasitism rate increased towards the middle of the year. An earlier study found stable parasitism rates throughout the season for bee and wasp nests, but the parasitism rates were correlated to equally stable abundances of the hosts (Osorio-Canadas et al., 2018), which we only see in bee nests.

On the one hand, both the parasitoids of the caterpillar-hunting and spider-hunting wasps are closely oriented to their hosts. On the other hand, temperature is very important for parasitoid activity (van Huis et al. 1994, Canevazzi and Noll 2011, Forrest and Chisholm 2017). Activity niches are different for different organisms. Bees, for instance, can be active at lower temperatures than their parasites, so that an increase in temperature can lead to an increase in parasitism rates (Forrest and Chisholm 2017). In line with hypothesis 4, we further found that the parasitism rate of wasps was rather temperature-dependent than humidity-dependent, in contrast to other findings suggesting that interactions between predators and parasitoids are usually driven by precipitation (Kishimoto-Yamada and Itioka 2015). Parasitism rates of caterpillar-hunting wasps increased with temperature in the colline zone and increased with temperature for spider-hunting wasps in the submontane zone if the relative humidity was not too high. For relative humidity, between 70 and 100%, the parasitism rate of spider-hunting wasps decreased with temperature, suggesting that humidity may become a limiting factor for parasitoids in combination with high temperatures.

The natural mortality, which is in our case mortality due to unknown reasons like extreme climatic conditions, pathogens, or little food provisions, showed similar seasonal patterns for bees, caterpillar- and spider-hunting wasps in the colline zone, contradicting hypothesis 3. Consistent with hypothesis 2, patterns differed in the submontane zone. Natural mortality increased with relative humidity for bees and caterpillar-hunting wasps, but for spider-hunting wasps only with simultaneous low temperature, according to hypothesis 4. Under high humidity conditions larvae and food provisions might be infected with pathogens, causing a higher mortality of the host. Simultaneously, the natural mortality rate decreased with temperature for bees and spider-hunting wasps if the relative humidity was high enough. But hot temperatures and low humidity at the same time could increase the risk of desiccation (Child 2007). Seasonal patterns of natural mortality are difficult to link to environmental factors as these are affecting the mortality rate during the whole development time, and not only during the phase of nest building as analysed here. Therefore, the results have to be interpreted with care.

Seasonality in life-history traits

Contradicting hypothesis 1, most patterns of life-history traits did not show seasonal variation. Nevertheless, the sex ratio of bees changed seasonally in the colline zone, with more males occurring at both the beginning and the end of the year. However, the sex ratio did not vary seasonally for any of the studied groups in the submontane zone. The strong dependence of bees on flowering plants was reflected in higher proportion of males when resource availability was low (Bosch 2008, Kümmerli and Keller 2011), in line with hypothesis 4. The higher proportion of males in correlation with lower amount of food resources has also been reported for wasps (Strohm and Linsenmair 1997), but in our study resources for wasps did not seem to be limiting in a way that the sex ratio was affected.

Development times tended to be similar for all trophic levels in contrast to hypothesis 3. It tended to be longer for bee, caterpillar-hunting and spider-hunting wasp nests constructed between April-May in the colline zone. Delayed emergence has been reported for bees and spider-hunting wasps in the tropics. It is assumed to be an apparent response to avoid the most inconvenient season of the year through a state of dormancy (Martins et al. 1999, Zanette et al. 2004, Sabino and Antonini 2017). Even though development times can vary between bee and wasp species and even within species, with some individuals showing direct development and others going into diapause (Martins et al. 2001, Buschini 2007), the development time seemed to be uniformly longer here. Between April and May, the larvae of all three groups needed between 100 to 200 days for their development to adults, even though the pattern was not seasonally significant in bees. This translated into an emergence period after the long rainy season between July-October.

Humidity played an important role in the development time of both wasp groups in the colline zone, with increasing air humidity leading to longer development times, according to hypothesis 4. Our findings hence suggest that an increase of humidity may trigger a kind of diapause to prevent the emergence of the brood in the long rainy season. Our results thus contrast previous findings, showing a decreasing development time with increasing relative humidity for a heteropteran host and its hymenopteran parasitoid (Cave and Gaylor 1988). Hence, the response of insects to ambient humidity may be different for parasitoids and depend on the host order and the range of humidity, with possibly more adverse effects at very low or high humidity levels. Furthermore, emergence in tropical insects is usually triggered by rainfall or high humidity (Wolda 1988), which should have resulted in development times bridging the long dry season in the colline zone. This seemed to be rather true for the spider-hunting wasps but not for the caterpillar-hunting wasps, which generally had a shorter development time during the long rainy season. But since the development time could only be estimated within a coarse timeframe, further studies are needed to answer how the life-history timing of tropical insects is matched to environmental conditions in areas with strong climatic seasonality.

Conclusion

Insects have to adapt to variable climatic conditions and resource availability in areas with clear seasonality, such as dry and rainy seasons. In this study, we investigated seasonal patterns of three functionally different Hymenoptera groups, i.e., pollinators (bees), first-order and second-order predators (caterpillar-hunting and spider-hunting wasps, respectively) in the colline and submontane zone of Mt. Kilimanjaro. We found strong seasonality in nest-building activity in all groups and both zones, while seasonal patterns were also reflected in different life-history traits and parasitism rates. Seasonal patterns were more often explained by climate and resources in the colline than the submontane zone. We did not find a consistent driver for seasonal patterns. Temperature, relative humidity, the interaction between temperature and humidity, and resource availability all correlated with different traits and insect groups. Therefore, a deeper study of ecological rates and life-history traits is indispensable to understand the diverse factors which shape insect communities under changing environmental conditions (Hopfenmüller et al. 2014). The interactive effects of elevational climate gradients and seasonality might be a useful approach to perceive possible future responses of insect communities to climate warming. At Mt. Kilimanjaro, seasonality in climate has changed during recent years, especially the character of the long rainy season (Otte et al. 2017). This may lead to immense challenges for insects that are closely adapted to seasonal changes and highlights the importance of taking a closer look when studying the seasonality in species abundance, traits, and interactions, especially in a world of rapid global change.

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Data Accessibility

The data will become publicly available via GFBio (https://www.gfbio.org/) according to the Rules of Procedure of the German Science Foundation (DFG).

Supplementary Material

The following materials are available as part of the online article at https://escholarship.org/uc/fb

Figure S1. Study area
Figure S2. Seasonal turnover in trap-nesting species compositions
Figure S3. Seasonal variation in survival rates and sex ratios- fitted models
Figure S4. Seasonal variation in all variables- fitted models and original data points
Figure S5. Seasonal variation of nests and parasitised brood cells- fitted models
Table S1. Seasonal variation of ecological rates and life-history traits- statistics
Table S2. Significant seasonal variations and correlations with climate and flower availability
Table S3. Species table

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