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Floral turnover and climate drive seasonal bee diversity along a tropical elevation gradient

Fairo F. Dzekashu[1,2] | **Abdullahi A. Yusuf**[2] | **Christian W. W. Pirk**[2] |
Ingolf Steffan-Dewenter[3] | **H. Michael G. Lattorff**[1] | **Marcell K. Peters**[3]

[1]International Centre of Insect Physiology and Ecology (ICIPE), Nairobi, Kenya

[2]Social Insects Research Group, Department of Zoology and Entomology, University of Pretoria, Pretoria, South Africa

[3]Department of Animal Ecology and Tropical Biology, Biocenter, University of Würzburg, Würzburg, Germany

Correspondence
Fairo F. Dzekashu
Email: fdzekashu@icipe.org;
fairodzekashu.f@tuks.co.za

Abstract

The contribution of seasonality in species communities to elevational diversity of tropical insects remains poorly understood. We here assessed seasonal patterns and drivers of bee diversity in the Eastern Afromontane Biodiversity Hotspot, Kenya, to understand the contribution of seasonality to elevational biodiversity patterns. Bee species and plant species visited by bees were recorded on 50 study plots in regrowth vegetation across four major seasons along two elevation gradients from 525 to 2530 m above sea level. Bees were sampled by transect walks using sweep nets and aspirators. We examined how local species richness (α-diversity) and seasonal changes in local species communities (β-diversity) contribute to species richness across seasons (γ-diversity) along elevation gradients. Using a multimodel inference framework, we identified the contribution of climate and floral seasonality to elevational patterns in bee diversity. We found that both α- and γ-diversity decreased with elevation. Seasonal β-diversity decreased with elevation and the high turnover of species across seasons contributed to a considerably higher γ- than α-diversity on study plots. A combination of seasonality in climate and the seasonal turnover of floral resources best explained the seasonality in bee species communities (seasonal β-diversity). We, therefore, conclude that, despite the more stable, and favorable climatic conditions in the tropics (in comparison to temperate regions), climatic seasonality and its influence on bees' floral resources largely determined seasonal patterns of bee species diversity along elevation gradients on tropical mountains.

KEYWORDS
β-diversity, climate change, Eastern Afromontane Biodiversity Hotspot, pollinators, regrowth vegetation, species distribution, tropical mountains

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H. Michael G. Lattorff and Marcell K. Peters contributed equally to this work.

INTRODUCTION

Conceptualizing the different processes that determine the distribution of species diversity along elevation gradients dates back two centuries ago (Von Humboldt, 1849), with a recent expansion of the field to new geographic areas, to less well-studied taxonomic groups of organisms, and to broader phylogenetic coverage of species communities (Cottenie, 2005; Kraft et al., 2011; Mori et al., 2013; Peters et al., 2016; Tang et al., 2012; Tello et al., 2015). The change in climate is a pervasive feature of elevation gradients, which ultimately determines many ecosystem properties from primary productivity to the diversity of species communities (Peters et al., 2019). Decreasing temperatures and climate-mediated variation in food resources have been identified as drivers of elevational diversity gradients for several insect taxa such as bees and cavity-nesting hymenopterans (Classen et al., 2015; Plowman et al., 2017), dung beetles (Gebert et al., 2019), and butterflies and moths (Maicher et al., 2018). One of the little-understood aspects of mountain ecology is how climatic seasonality, here defined as the changes of climatic conditions within the year, contributes to trends of species diversity along elevational gradients (Körner, 2007). This is particularly true for tropical mountains, which host the most extreme gradients in climate and species diversity and on which the consequences of seasonality remain little studied (Körner, 2007).

Seasonality in temperature and precipitation has a significant impact on the phenology of plants and the physiology of animals at high and low latitudes (Thuiller, 2007). At high latitudes, low temperatures are the most limiting factor for species developmental processes and activity, leading to an often pronounced climate seasonality and phenology (Collins et al., 2013; Qian et al., 2013). In contrast, seasonal patterns in the tropics are often more subtle and strongly related to changes in precipitation over the year (Maicher et al., 2018). Tropical seasonality is often considered less extreme as the climatic conditions in most areas do not generally limit ectothermic metabolism and the net primary productivity of ecosystems (e.g., frost). However, due to the narrower climatic niches of tropical species (Janzen, 1967), relatively small changes in climate may lead to significant changes in the activity patterns of species. This is true for most arthropods with short life cycles (Maicher et al., 2018; Schmitt et al., 2021), for example, bees.

Determining the mechanisms shaping seasonal distribution of organisms on tropical elevation gradients has been a daunting task to achieve due to the challenging nature of the terrain and rigorous sampling effort required. Therefore, focusing on specific taxa with known contributions to ecosystem function (e.g., bees) becomes very important. Bees are important as they contribute significantly to the provision of pollination services (Blüthgen et al., 2007; Potts et al., 2003; Steffan-Dewenter & Tscharntke, 2001). They are sensitive to changes in climate and to available flowering plant resources (Classen et al., 2015) and show clear patterns of abundance and diversity that deviate from other organisms. Therefore, determining the mechanisms shaping any observed seasonal patterns in bee assemblages would serve as the baseline to understand seasonal dynamics and the underlying mechanisms shaping patterns in other taxa.

Along elevation gradients, mean annual temperature (MAT) decreases, while precipitation shows variable changes with elevations (Körner, 2007). This fluctuation in climate may vary with seasons and would exert an influence on species composition. On high latitude mountains, seasonal temperature changes cause monotonic declines in the season length in plant and animal communities along the elevation gradient, while tropical mountains in humid areas often show reduced seasonality due to the generally high and more stable temperatures (Körner, 2007). On tropical mountains with a dry base, seasonality is often higher in the lowlands as high temperatures and low rainfall may cause temporal aridity (Körner, 2007) or because temperatures may even temporally exceed thermal thresholds of organisms (Araújo et al., 2013). Seasonal changes in climate may directly or indirectly influence species communities. In case of variation in the climatic niches of local species, a high seasonality in climate may cause a seasonal turnover (Williams et al., 2017) or seasonal decreases of species richness in communities. Climatic factors also impose physiological constraints on organisms resulting in them occupying attenuated ranges (Archibald et al., 2013; Janzen, 1967), along elevational gradients.

In addition, climatic changes may lead to a turnover in the type and quantity of food resources available to bees. Seasonal variability of food resources plays a pivotal role in the assembly patterns of corresponding dependent species (González et al., 2009). High plant species diversity can provide diverse niche habitats necessary for the coexistence of diverse bee assemblages (Potts et al., 2003) and control of microclimate (Knapp et al., 2002; Schnitzer, 2005). Seasonal shifts in the type and quantity of food resources may induce a consequent shift in the species composition of consumer communities, especially for organisms showing some degree of specialization on specific food resources (Tilman et al., 1997). Therefore, seasonality in climate may influence the total number of

species living in an ecosystem over the year (Williams et al., 2017).

In this study, we examined patterns and drivers of seasonality in bee assemblages and the contribution of seasonality to the total number of species observed over an entire year along a tropical elevation gradient in the Eastern Afromontane Biodiversity Hotspot (EABH) in Kenya, East Africa. In temperate climate zones, bees show clear phenologies in activity patterns (Leong et al., 2016). For tropical bee communities, climatic gradients such as the changes of temperature and precipitation along elevation gradients have been reported as drivers of bee diversity on mountains (Classen et al., 2015). Studies on β-diversity have largely examined variation in space (Kraft et al., 2011; Samnegård et al., 2015; Tello et al., 2015). However, there is lack of empirical data quantifying patterns and drivers of seasonal changes in species composition (see Maicher et al., 2018, 2020) and its contribution to the total number of species in ecosystems. While some bee species are known to be generalists regarding the plant species they visit for collecting pollen and nectar (Bartomeus et al., 2011), some show a strong dependence on specific host plants (Haider et al., 2014; Larkin et al., 2008; Müller & Kuhlmann, 2008) making some degree of seasonal tracking of floral resources likely (Wood et al., 2018). Nonetheless, it remains unknown to what degree seasonal trends in bee communities along tropical elevations correspond to changes in floral resources or climate.

In this study, we aimed at understanding the seasonality in bee communities along East African elevation gradients. We, first, reveal changes in seasonal β-diversity of bees along elevation gradients and quantified its contribution to the total number of bee species observed over the year (γ-diversity). Second, we analyze the causes of seasonal β-diversity in bee communities, by disentangling the effects of changes in climate and in the composition of flowering plant communities across seasons.

METHODS

Study area and time of study

Our study was carried out from July 2019 to April 2020 along two elevation gradients in Kenya, one elevation gradient of 525–1865 m above sea level (asl) in the Taita Hills region (38°10′ to 39°03′E, −3°15′ to −4°0′S) and one along a 1470–2530 m asl in Murang'a County, the central region of Kenya (0°34′ to 1°5′S, 36°43′ to 37°27′E; Figure 1). Both elevation gradients are situated within the Eastern Afromontane Biodiversity Hotspot (EABH). The lowland in this region has a subtropical

climate comprising arid and semiarid conditions, while the highlands are categorized into montane forests. Farming and grazing activities are intermixed at some distances into the forest areas forming a multiplex of diminutive variegations, with each site comprising of a set of specific multifarious anthropogenic activities. The landscape matrix along the elevation gradient consists of savannah, shrubland, indigenous bushlands, pasture, and human settlement with subsistence agricultural activities with crops such as coffee, mangoes, cassava, tomatoes, banana, maize, pepper (*Capsicum anum*), cabbage, spinach, cucumber (*Cucumis sativus*), and beans. Subsistence farms are accompanied by large-scale agricultural plantations such as tea (*Camelia sinensis*) and pineapple plantations in Murang'a and sisal (*Agave sisalana*) in Taita.

Mean annual precipitation increases and MAT decreases with elevation (Appendix S1: Figure S1) such that the climate becomes more humid and allows the growth of premontane and montane forests on mountain tops. Rainfall shows a bimodal seasonal pattern with a short-rainy period between November and December, followed by a dry period of 2–3 months, while prolonged heavy rainfalls typify the periods from March to May ensued with a long-dry period of 5 months. The mean annual rainfall ranges from approximately 250 to 2000 mm (Orodho, 2006) from low 525 m to high 2530 m asl elevations, with mists coverage on the higher elevations in most part of the year (Pellikka et al., 2009) even in the absence of rain. Across the entire region, temperature ranges from approximately 17.5 to 19°C and approximately 29 to 31°C for mean annual minimum and mean annual maximum temperatures, respectively (Gebrechorkos et al., 2019), and varies with seasonality in temperature and precipitation. Precipitation seasonality is mostly stable across a larger part of the lowlands for up to about 1500 m before steadily decreasing toward the higher elevations. Meanwhile, seasonality in temperature increases sharply to about 800 m in the low elevations and declines nonlinearly along the higher elevations (Appendix S1: Figure S1).

We established 25 study plots of 100 × 100 m along each elevation gradient, making up a total of 50 study plots (Figure 1). Study plots were always positioned in regrowth vegetation, ensuring a minimum geographic distance of 2.3 km from each other (taking into consideration the average foraging range of most tropical bee species, e.g., Wikelski et al., 2010) and following approximate elevation increments of about 100–250 m between neighboring plots. A large and increasing portion of land area in the tropics can be classified as anthropogenic influenced "regrowth vegetation." This vegetation was established by subsistence farming and
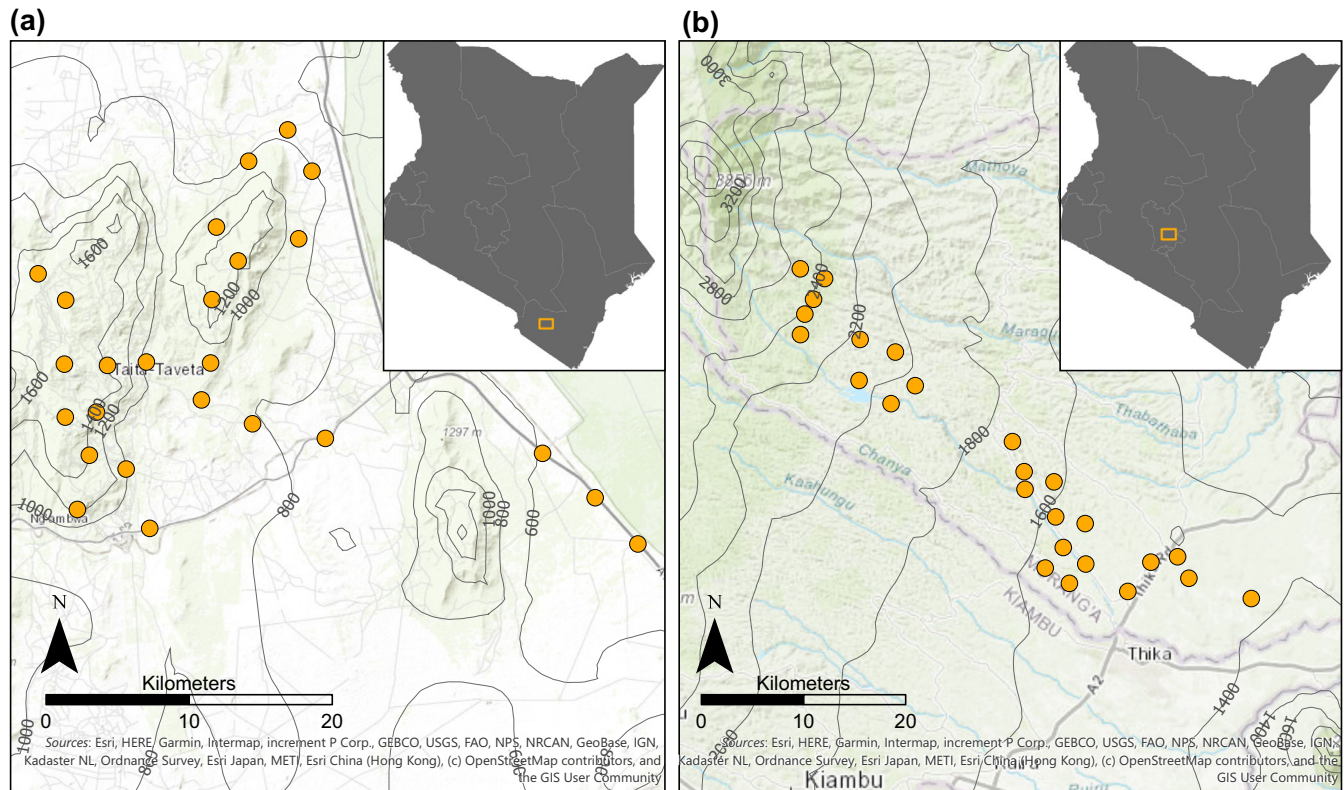
FIGURE 1 Map of the study sites. This map shows the geographic position of study plots (orange dots) along elevation gradients in Taita Hills (a) and Murang'a (b) in Kenya (inserted figures). Each gradient consisted of 25 study plots. Contour lines in the background show elevation levels

grazing activities replacing the natural vegetation and is characterized by natural herbs and woody plants regrowing intermixed with single or few large trees (Appendix S1: Figure S2). It has been demonstrated that regrowth vegetation can contribute to overall landscape heterogeneity, structural complexity, and the conservation and restoration of rare species (Tscharntke et al., 2011).

Bee sampling

Bee sampling was conducted four times intermittently between July 2019 and April 2020, corresponding to the four major seasons described above (November and December: short-rainy and warm season, March–April: long-rainy and warm season, July: long-dry and cold season, September–October: short-dry and cold season). Bees were collected by standardized sweep netting and suction with a Prokopack aspirator (Model 1419, John Whock, Gainesville, FL, USA).

Sampling was congruous and standardized for each site. Each plot was visited once per season by three experienced observers (always the same) for 2 h during the peak activity time of bees (between 9:00 AM and 5:00 PM). We ensured equal sampling probabilities by

exclusively conducting sampling during rain-free periods without or with a shallow wind. During sweep netting, a slow, gentle, and parallel movement around the entire plot was conducted, sampling all bees during flight on plant flowers. For taller plants that were inaccessible or sweep netting was not possible, we collected bees from flowers using an Improved Prokopack aspirator (Model 1419, John Whock, Gainesville, FL, USA). This tool made it possible to collect bees from trees up to ~4 m in height. All sampled bees were frozen directly in the field by transferring them into a −18°C motorable cooler (Waeco Coolfreeze CF-35, Dometic GmbH, Emsdetten, Germany) before onward transfer to a −80°C freezer in the laboratory. The African subspecies of the Western honeybee (*Apis mellifera* L.) were not included in the analysis because we were interested in the diversity of wild bees (e.g., Powney et al., 2019), which are known to enhance the ecosystem services of pollination independently of honeybees (Garibaldi et al., 2013) and also because beekeepers introduced most honeybee colonies in the region. Identification of the specimens was done using a Zeiss microscope affixed with an Axiocam 105 color camera (Carl Zeiss microscope, Jena, Germany). Bees were identified to the genus level following Michener (2007) and Eardley et al. (2010). Specimens were sorted to either

species or morphospecies level with the help of an expert from the National Museums of Kenya.

Assessment of the diversity of bee-visited plants

In order to estimate the available floral resource diversity for bees, we counted on each study plot during each sampling period the number of flowering plant species visited by bees. During the 2-h sweep netting walks (for collecting bees), all flowering plant species on which a bee was touching the reproductive structures (anthers or stigma) were recorded. All visited plants were photographed using a standard digital camera while in the field, and samples of each species were collected to establish a herbarium. All plant samples were later identified to species level by an experienced plant taxonomist at the National Museums of Kenya.

Climatic variables

We extracted four different climatic variables from the Climatologies at High-Resolution for the Earth's Land Surface Area (CHELSA) database (Karger et al., 2017), particularly the bioclimatic variables supplied in the BIO-CLIM data. This data set provides climate data at a resolution of $30''$ ($\sim$1 km^2). We derived the following climate variables: BIO1: mean annual air temperature (MAT), BIO4: seasonality of temperature, which considers changes in temperature in a year ($T_{seasonality}$); BIO12: mean annual precipitation (MAP); and BIO15: seasonality in precipitation, which is the fluctuation of precipitation in a normal year ($P_{seasonality}$). For a complete description of parameters used, see Appendix S1: Table S1. This database has been widely used in recent ecological studies (e.g., Boyer et al., 2020; Brown et al., 2018; Ivajnšič & Devetak, 2020; Marcondes et al., 2020; Pironon et al., 2019; Powell et al., 2018) and is particularly robust in providing more realistic precipitation data for mountainous areas in comparison with other databases (Karger et al., 2017).

Statistical analyses

Statistical analyses were conducted within the R statistics platform version 4.0.3 (RStudio Team, 2021) using the following packages: "vegan," "mgcv," "MuMIn," and "corrplot."

To assess the cumulative number of species over the whole study time and for different seasons, we constructed species accumulation curves using the "vegan" package to assess the completeness of sampling. In order to test whether changes to a more humid and warmer climate is associated with contractions or expansions of elevational ranges of species, we calculated, for the subset of species which were present in both wet–warm and dry–cold seasons, the average differences in species elevational ranges. Using a one-sample t test, we tested whether average differences in elevational ranges differed from 0.

To determine trends in species diversity with elevation and to assess the effects of seasonality on species diversity in different elevations, we used additive partitioning of species diversity (Lande, 1996). Alpha diversity (α) was here defined as the mean species richness per plot observed across the four seasonal samplings, and gamma diversity (γ) was defined as the cumulative species richness per study plot across all seasons, with beta diversity (β), in general, describing the change in species composition per plot per season. We here used several definitions of β-diversity reported in the literature:

1. Additive β-diversity, given as $\beta_{ADD} = \gamma - \bar{\alpha}$.
2. Multiplicative β-diversity given as $\beta_w = \gamma/\bar{\alpha}$ (Whittaker, 1960, 1972).
3. Beta partitioning, given as $\beta_p = 1 - \bar{\alpha}/\gamma$ (e.g., Kraft et al., 2011)
4. Additive beta deviation (β_d), controlling for differences in γ-diversity (Kraft et al., 2011).

To calculate the β_d, we used the null model approach developed by Kraft et al. (2011). In this approach, β_{ADD} was first calculated by repeatedly and randomly shuffling individuals among seasons while preserving γ-diversity, the relative abundance of species at the location, and the number of individuals per seasonal sample. In a second step, this null model estimate was subtracted from the observed additive β-diversity to generate the additive β-deviation (β_d), a measure of additive β-diversity, which is independent of the variation in γ-diversity. The null model concept of Raup and Crick (1979) is the model of choice in correcting for species pool effects (α- and γ-dependencies) and improving interpretations of β-deviations from null expectations (e.g., Chase et al., 2011; Kraft et al., 2011).

To obtain a measure of the diversity of plant species visited by bees on-site, we calculated the alpha (F_α), gamma (F_γ), and subsets of β-diversity measures, that is, β-multiplicative ($F_{\beta w}$), β-additive ($F_{\beta ADD}$), and β-partitioning ($F_{\beta p}$) diversity as described for the bees above.

To assess whether changes in β-diversity of bees with elevation are mainly due to a loss of species or due to the turnover of species, we calculated the Jaccard dissimilarity (β_j) and its turnover $\beta_{j\text{-turnover}}$ and nestedness ($\beta_{j\text{-nestedness}}$) components following Baselga (2012).

We used generalized additive models (GAM) to examine the relationships between diversity measures (α, γ, β_w, β_{ADD}, β_p, β_d, β_j, $\beta_{j\text{-turnover}}$, and $\beta_{j\text{-nestedness}}$) with elevation. GAM uses a nonparametric regression approach using smoothing (splines) functions to pervade simple and complex nonlinear and linear relationships (Wood, 2006). GAMs were computed using the "gam" function in the *mgcv* package and data family set to Gaussian type with an "identity" link function. The basis dimensions were set to five ($k = 5$), circumventing the effects of trend over-parameterization (Peters et al., 2016).

After finding patterns in bee diversity with elevation, we further assessed which environmental factor(s) most likely determined changes in α-, β-, and γ-diversity and analyzed the influence of climatic (MAT, MAP, $T_{seasonality}$, and $P_{seasonality}$) and flower diversity (F_α, F_β) parameters on bee diversity (α, γ, and β) using ordinary linear models and model selection based on the Akaike's information criterion (AIC). Since our sample size was small compared to the estimated parameters ($n/K < 40$), we used the second-order AIC_c rather than the original AIC (Burnham & Anderson, 2002) to derive the support for individual models. All explanatory variables and dependent variables were standardized by *z*-transformation, allowing a direct comparison of effect strengths among explanatory variables. We constructed a full model for each response variable, including both climate and plant diversity variables and calculated AIC_c values for these and all nested models. We compared all models showing a ΔAIC_c <2 to the best-selected model (Appendix S1: Table S2).

RESULTS

Species diversity of bees and bee-visited plants

We recorded 3137 individuals of wild bees belonging to 185 (morpho)species (Appendix S1: Table S3.1) from five bee families. The family Apidae was the most abundant and most species-rich (43.1% of all individuals, 17 genera, 84 species), followed by the family Halictidae (40% of individuals, nine genera, 55 species), Megachilidae (14.7% of individuals, six genera, 40 species), Colletidae (2% of individuals, two genera, five species), and Andrenidae (only five individuals from one genus and one species). The cumulative number of species increased with the number of sampling periods (Figure 2a). The cumulative number of sampled species was lower in the dry and cold (75 and 66 species) than in the wet and
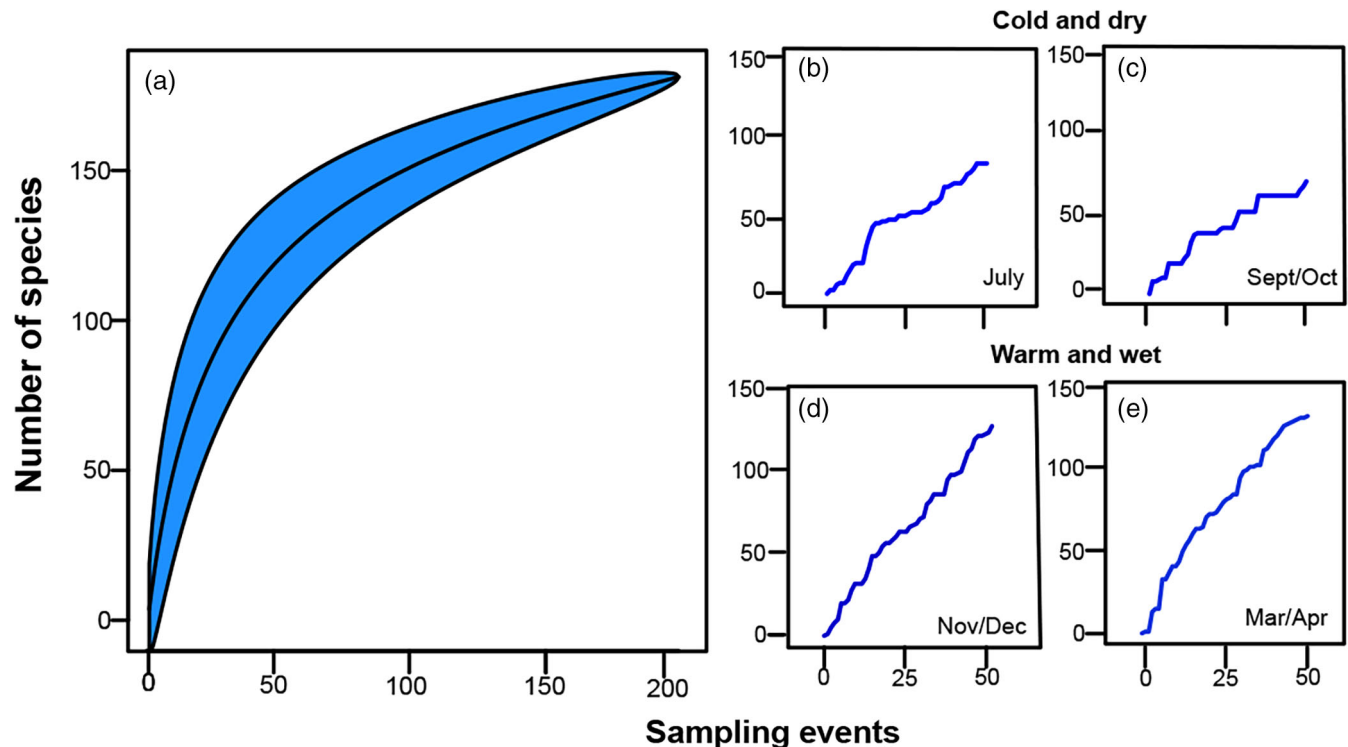
FIGURE 2 Species accumulation curves across all seasons (a) and for each season separately (b–e). (a) The mean and 95% confidence interval of the cumulative number of species for a given number of samples were calculated by 200 random shuffling of samples from all four seasons and for each season (i.e., cold and dry: b,c; and warm and wet: d,e). The lines in (b–e) show the cumulative number of species separately for each season, following the order in which study plots were visited

warm (129 and 136 species) seasons (Figures 2a–e). Comparing the elevation ranges of bee species in the wet–warm and the cold–dry seasons revealed that the elevational range was on average 312 m (one-sample t test, $p < 0.01$) larger (i.e., elevational range expansion takes place) in the former than in the latter (Appendix S1: Figure S3).

We recorded 312 plant species, 173 genera, and 55 families visited by bees along the elevational gradients. The five most species-rich families on which we recorded bees feeding on were the Asteraceae (27 genera and 48 species), Fabaceae (21 genera and 41 species), Lamiaceae (16 genera and 32 species), Malvaceae (five genera and 17 species), and Poaceae (11 genera and 12 species) (Appendix S1: Table S3.1).

Effects of elevation on species diversity

The alpha (α) and gamma (γ) diversity of bees declined linearly and significantly with elevation (Figure 3a,b) (α-diversity: $n = 50$, estimated degrees of freedom [edf] of the smooth term = 1, $F = 5.4$, $p < 0.05$, γ-diversity, $n = 50$, edf = 1, $F = 13.4$, $p < 0.001$). However, there was a very high variation in observed α- and γ-diversity such that the explained deviance (ED) was rather low (α-diversity: ED = 10.2%, γ-diversity: ED = 21.8%). The seasonal bee diversity (β-diversity) declined significantly with elevation irrespective of the type of β-diversity measured (Figure 3c; GAMs based on a sample size of $n = 50$: β_{ADD}: ED = 27.6%, edf = 1, $F = 18.31$, $p < 0.001$; β_w: ED = 26.3%, edf = 1.88, $F = 6.85$, $p = 0.01$; β_p: ED = 27.2%, edf = 1.82, $F = 7.51$, $p = 0.01$; β_j: $n = 50$, ED = 27.2%, edf = 1.8, $F = 7.4$, $p = 0.01$). Even after accounting for the variation in γ-diversity (Kraft

et al., 2011), seasonal β-diversity decreased with elevation (β_d: $n = 50$, ED = 16.4%, edf = 1, $F = 9.4$, $p < 0.01$). Decomposing β_j into turnover and nestedness revealed that the seasonal turnover in bee communities decreased with elevation, while the nestedness increased with elevation (Figure 4; turnover: $n = 48$, ED = 28.2%, edf = 1.5, $F = 8.4$, $p < 0.001$; nestedness: $n = 48$, ED = 16.1%, edf = 1, $F = 8.8$, $p < 0.01$). Generally, the seasonal turnover of species was far more important for the seasonality in bee communities than the nestedness; that is, the bee species present on a study plot in a certain season were not a subset of the species during the most diverse season but communities rather composed of different species.

Determinants of species diversity

Both climatic variables and floral resources significantly affected bee species diversity, but the type and magnitude of effects differed between response variables as shown in Figure 5. Despite the strong residual variation in bee diversity patterns (α-, β-, and γ-diversity) along the elevation gradients (Figure 3a–c), the variation explained by a combination of climate and plant diversity variables was rather high (Figure 5).

Bee α-diversity was strongly and significantly predicted by both MAT and flower alpha diversity (F_α) with α-diversity of bees increasing with both MAT and the α-diversity of bee-visited plants (Appendix S1: Table S2). γ-diversity of bees increased with MAT, with the α-diversity of bee-visited plants and was higher in study plots showing pronounced seasonality in climate (higher levels of $T_{seasonality}$ and $P_{seasonality}$) (Figure 5).
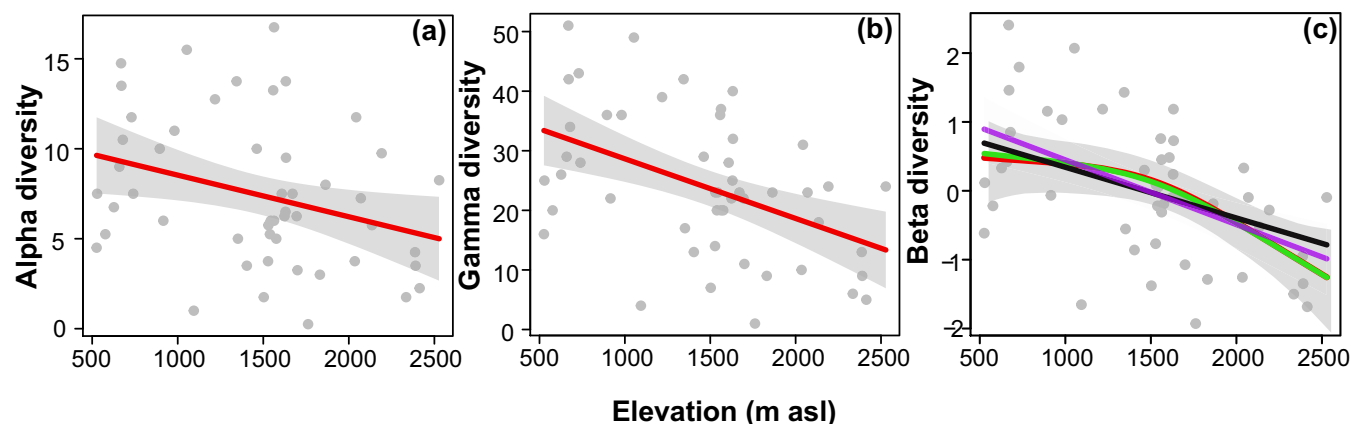
FIGURE 3 Patterns of bee species diversity along elevation gradients. (a) Mean ($\pm$95% confidence interval) α-diversity, (b) γ-diversity, and (c) different measures of β-diversity (β_w, β_{ADD}, β_p, and β_d) denoted by red, purple, green, and black lines, respectively. All diversity trends were analyzed using generalized additive models (Gaussian family, basis dimension $k = 5$). Dots in (a and b) show the observed mean α- and γ-diversity per study plots, respectively. Dots in (**c**) depict measures of the additive β-deviation per study plot
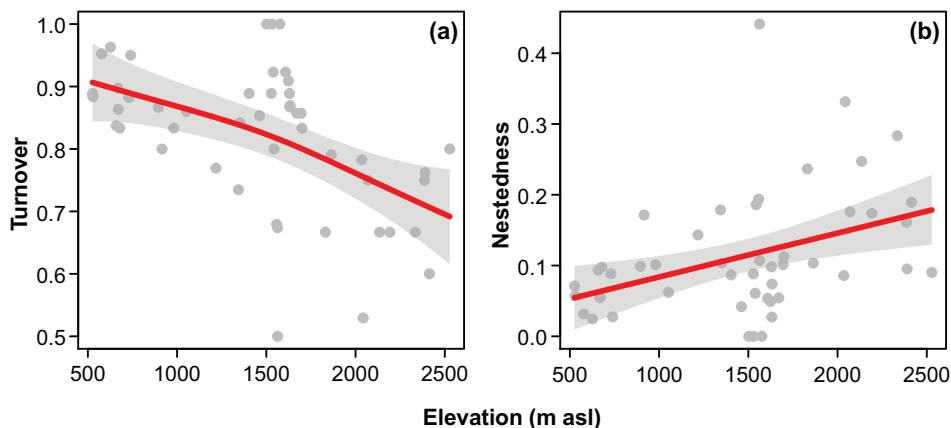
FIGURE 4 Patterns of seasonality in species composition with elevation. (a) Patterns of seasonal species turnover (ranges from 0 to 1) with elevation. High values indicate that a seasonal change of species mainly drives seasonal β-diversity on study plots with species differing among seasons. (b) Patterns of nestedness in species communities (ranges from 0 to 1) with elevation. High values indicate the species communities in species-poor seasons are nested subsets of those found in the species-rich season. All diversity trends were analyzed using generalized additive models (Gaussian family, basis dimension $k = 5$). Dots represent observed values of turnover and nestedness per study plot
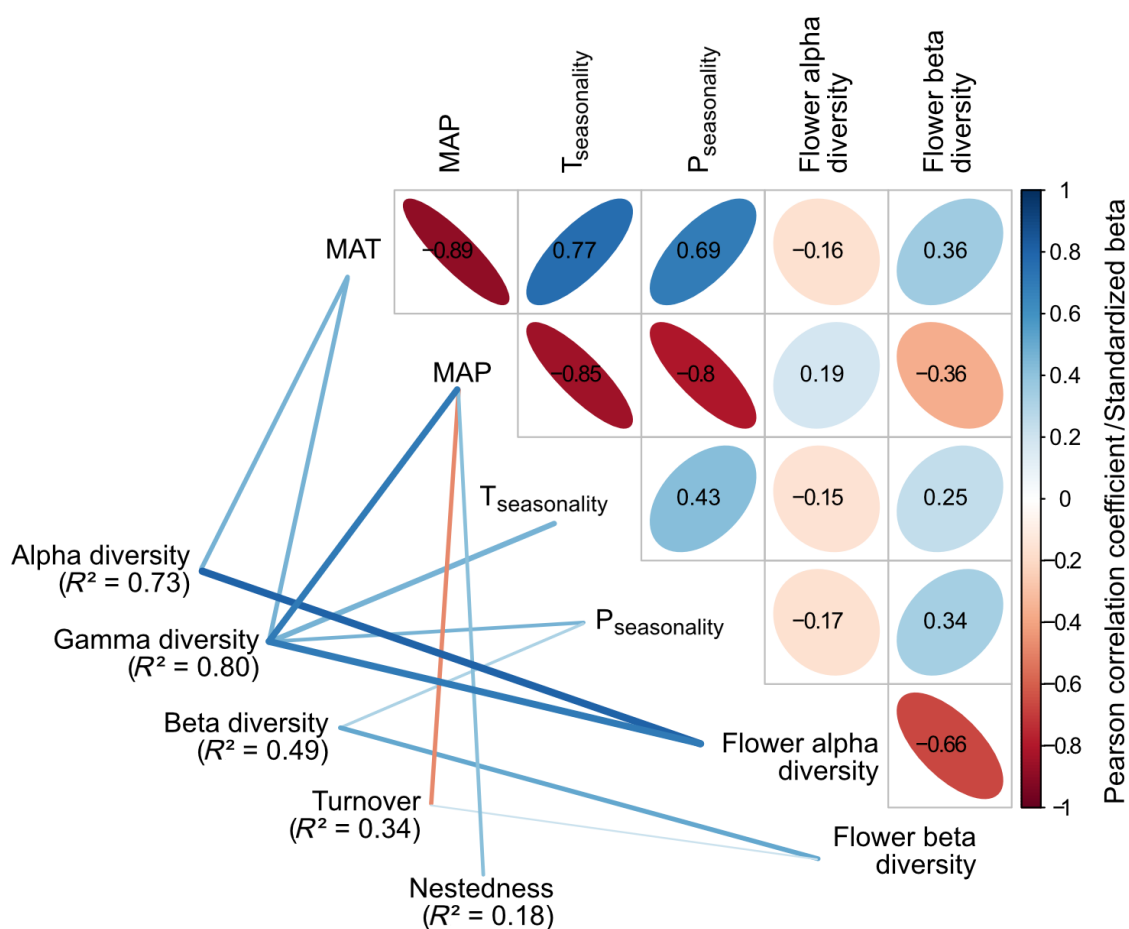
FIGURE 5 Summary of best fit models. This indicates the significant drivers (predictors) of bee diversity along the elevation gradients for different diversity measures. The "boldness" of each link denotes the relative strength of an association, while the colors blue and red denote positive and negative interacting effects, respectively. The relative amount of explained variance or coefficient of variation (R^2) is given for each response variable. The correlation matrix (correlogram) on the right underscores the direction and strength in the relationship between explanatory variables

The seasonal β-diversity of bees increased with the seasonality in climate ($P_{\text{seasonality}}$) and the β-diversity of floral resources, indicating that β-diversity in bee communities was higher on study plots showing a strong seasonality in both climate and plant community composition. Concerning the turnover and nestedness components of β-diversity, we found that species turnover increased positively and linearly with the β-diversity of plant communities ($F_{\beta m}$), and it decreased with increasing rainfall (MAP). In contrast, the nestedness component of β-diversity increased significantly with MAP. For most response variables, the most relevant drivers of diversity measures were consistent among competing models ($\Delta AIC_c < 2$), but there was a high inconsistency in the explanatory variables for nestedness among the competing models (Appendix S1: Table S2).

DISCUSSION

Previous studies on β-diversity along elevation gradients have focused on spatial aspects (see Kraft et al., 2011; Mori et al., 2013; Tang et al., 2012; Tello et al., 2015). Here, we calculated several β-diversity statistics, including a null model approach suggested by Kraft et al. (2011) to analyze the seasonal turnover of bees and plants and its contribution to the total bee diversity across the full year. Our study revealed pronounced seasonality in wild bee assemblages, which significantly contributed to patterns of elevational diversity. Seasonal changes in bee assemblages were highest in the lowlands and declined with elevation and were driven both by seasonal shifts in climate and by the turnover of the flowering plant communities.

We found that seasonal changes in bee communities strongly contributed to γ-diversity. The total number of bee species found on study plots across all seasons was ∼2.5 to ∼3.5 times higher than the average number of species found within single seasons. Floral resource availability and climate seasonality are known to affect bee assemblage patterns, with higher diversity and turnover in species composition recorded in wet than in dry seasons (Escobedo-Kenefic et al., 2020; Samnegård et al., 2015). The contribution of seasonality effects (i.e., seasonal β-diversity) to γ-diversity was not homogeneous but decreased with elevation. While seasonal β-diversity in insect communities along tropical elevation gradients remains little studied, a number of studies on spatial β-diversity also point to a general decrease with elevation (e.g., Plowman et al., 2020; Tang et al., 2012). The consistently high contribution of β-diversity to γ-diversity and the decrease of β-diversity with elevation points to a high importance of seasonality for the establishment of diversity gradients of bees on tropical mountains.

Furthermore, the severe dryness in vegetation at the lower arid elevations throughout the long-dry and short-rainy seasons (Appendix S1: Figure S2), left only a few species to thrive in these severe conditions and across a large elevation range. This was true for members of the genera *Seladonia* (*Halictus*), *Braunsapis*, and *Patellapis*, where species exhibited a shift to areas with suitable habitats while gaining in overall distributional range. This severe dry condition also led to alternations in elevational range occupancy of some species (e.g., *Amegilla* spp. and *Megachile* spp.) into the higher elevations (e.g., Appendix S1: Table S3.1), while other low elevation species (e.g., *Lipotriches* spp.) only reemerged during the short-dry and long-rainy periods when foraging resources became available.

The seasonal β-diversity of bees declined significantly with elevation irrespective of the type of β-diversity measure used. Seasonal β-diversity still decreased with elevation even after controlling for γ-diversity (Kraft et al., 2011). Our result reveals that the change in β-diversity with elevation was driven by a seasonal shift in floral resources and seasonality in precipitation, which both positively influenced β-diversity of bees. This result highlights the impact of floral resource heterogeneity across seasons, suggesting associations of bee species with specific flowering plant species (Muller, 1996). This temporal turnover in bee activity reduces interspecific competition for floral resources (Michener, 1979; Velthuis, 1992). Apart from the change in floral resources, precipitation seasonality significantly explained seasonal β-diversity of bees. This suggests that the activities and phenology of bee species in the region are restricted to certain climatic conditions occurring in parts of the year, whereas some bees restrict their activity to the colder and drier parts of the year (Straka et al., 2014) and the activity of others peaks in the warm and wetter periods (Willmer & Stone, 2004), thus contributing to the high seasonality (β-diversity) in bee assemblage patterns.

The α-diversity significantly declined with elevation and could be well explained by an interplay of the α-diversity of floral resources and MAT, which both had a positive effect ($R^2 = 73\%$). This finding corroborates previous studies on bees and cavity-nesting hymenopterans, which found close associations of species richness with temperature and the availability of floral resources (Abrahamczyk et al., 2011; Classen et al., 2015; Ebeling et al., 2008; Escobedo-Kenefic et al., 2020; Fisher et al., 2017; Mayr et al., 2020; Potts et al., 2003). The positive effect of MAT on species richness can be explained by higher metabolic rates of ectothermic organisms under high temperature, fostering net energy intake, and population growth (Brown et al., 2004; Classen et al., 2015; Savage et al., 2004). Furthermore, higher temperatures are associated with higher rates of molecular evolution

and diversification (Allen et al., 2006; Eiserhardt et al., 2013; Lin et al., 2019) producing positive relationships between temperature and species richness.

When partitioning seasonal β-diversity into the components of species turnover and nestedness, we found the former to be generally more important than the latter across the elevation gradient. Furthermore, while species turnover decreased with elevation, nestedness increased. In high elevation areas, with high levels of MAP and low temperatures, bee communities in species-poor seasons were to a larger degree subsets of those in species-rich seasons, in contrast, under the drier and hotter conditions in the lowlands, bee species more strongly shifted across different seasons, revealing divergent mechanisms of seasonal community assembly from low to high elevations (Walther, 2010). The effects of abiotic stressors such as low temperatures coupled with wet soils, which become increasingly prominent at higher elevations (Körner, 2007; Lundquist & Loheide, 2011; Nogués-Bravo et al., 2008; Rahbek, 1995), constrain the activity of local species to few seasons with no replacement by other species in the climatically harsh parts of the year (Colwell et al., 2008). This could be an explanation for the increasing contribution of the nestedness component of β-diversity in bee species assemblages at higher elevation.

Our study had some caveats. First, while it revealed the importance of climatic and floral resource seasonality on bee species diversity along tropical elevation gradients, it allowed only the assessment of seasonal trends over 1 year. As seasonal trends may have an interannual variation, a study on seasonal trends spanning multiple years could reveal a more detailed picture of the seasonality in bee communities on African mountains. Second, on the studied elevation gradient, MAT and MAP and their seasonality were rather strongly correlated, which could cause problems in causal inference. We handled this by reporting the degree of correlation for these and all other explanatory variables and by using multimodel inference to derive the support for explanatory variables. Strong correlation among explanatory variables would here lead to multiple alternative competitive models, which we documented in Appendix S1: Table S2. Comparisons among competitive models revealed, however, consistent support for most effects and diversity measures except for the nestedness component of β-diversity, for which model uncertainty was high.

CONCLUSION

We showed that climatic seasonality and its influence on bees' floral resources largely determined seasonality patterns of bee species diversity along elevation gradients on tropical mountains. Our results further revealed that a potentially reduced seasonal variation in rainfall and more homogeneous plant communities in the course of global change could lead to a loss of bee diversity on mountains in East Africa. As important as hotspots and mountainous areas are in harboring endemic species, understanding the impact and consequences of climatic change in shaping the vegetation structure of this region would be crucial for the conservation of bee pollinators in the coming decades.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT
Data (Dzekashu, 2021) are available from Figshare: https://doi.org/10.25403/UPresearchdata.17091020.v1

ORCID
Fairo F. Dzekashu https://orcid.org/0000-0003-2367-4027
Abdullahi A. Yusuf https://orcid.org/0000-0002-8625-6490
Christian W. W. Pirk https://orcid.org/0000-0001-6821-7044
Ingolf Steffan-Dewenter https://orcid.org/0000-0003-1359-3944

H. Michael G. Lattorff https://orcid.org/0000-0002-8603-6332

Marcell K. Peters https://orcid.org/0000-0002-1262-0827

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