

Original Articles

Network resilience of plant-bee interactions in the Eastern Afromontane Biodiversity Hotspot

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ARTICLE INFO

Keywords:

Ecosystem stability
Pollinators
Insect conservation
Recovery rates
Climate change
Tipping points
Ecosystem services
Elevation gradient
East African mountains
Kenya
Tropics

ABSTRACT

Interaction network resilience can be defined as the ability of interacting organisms to maintain their functions, processes or populations after experiencing a disturbance. Studies on mutualistic interactions between plants and pollinators along environmental gradients are essential to understand the provision of ecosystem services and the mechanisms challenging their network resilience. However, it remains unknown to what level ecological changes along climatic gradients constrain the network resilience of mutualistic organisms, especially along elevation gradients. We surveyed bee species and recorded their interactions with plants throughout the four major seasons (i.e. long and short rainy, and long and short dry) on 50 study sites positioned along an elevation gradient (525 m to 2,530 m asl) in the Eastern Afromontane Biodiversity Hotspots in Kenya, East Africa. We calculated bee and plant network resilience using the network resilience parameter (β_{eff}) and assessed changes in bee and plant network resilience along the elevation gradient using generalised additive models (*gams*). We quantified the effects of climate, bee and plant diversity, bee functional traits, network structure, and landscape configuration on bee and plant network resilience using a set of multi-model inference frameworks followed by structural equation models (SEM). We found that bee and plant species exhibited higher levels of network resilience at higher elevations. While bee network resilience increased linearly across the elevation gradient, plant network resilience increased exponentially from ~1500 m and higher. Bee and plant network resilience increased in areas with reduced mean annual temperature (MAT) and decreased in areas with lower mean annual precipitation (MAP). Our SEM model showed that increasing temperatures indirectly influenced plant network resilience via network modularity and community assemblage of bees. We also found that MAP had a direct positive effect on plant diversity and network resilience, while the fragmentation of habitats reduced richness of plant communities and enhanced network modularity. In conclusion, we revealed that mutualistic networks showed higher network resilience at higher elevations. We also unveiled that climate and habitat fragmentation directly or indirectly influences the network resilience of plants and bees via the modulation of community assemblages and interaction networks. These influences are lower at higher elevations such that these systems seem better able to buffer against extinction cascades. We thus suggest that, management efforts should be geared at consolidating natural habitats. In contrast, restoration efforts should aim at mitigating climate change effects and harnessing the ability of mutualists to reconnect broken links to improve the network resilience and functioning of East-African montane ecosystems.

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1. Introduction

Mutualistic interactions such as those between plants and pollinators are important in sustaining biodiversity and the stability in plant-pollinator communities (Huang et al., 2021). Interaction network resilience can be defined as the ability of interacting organisms (e.g. plant-pollinators) to maintain their functions, processes or populations after experiencing a disturbance. (see Holling, 1973; Kaiser-Bunbury et al., 2010). Mutualistic interaction network resilience (hereafter: network resilience) is important as it sustains the smooth flow of ecosystem services in different and rapidly changing environments. However, as anthropogenic activities continuously modify the ability of ecosystems to buffer perturbations, this would eventually lead to a reduction in essential ecosystem services crucial for our well-being (Elmqvist et al., 2003). Over the last two decades, studies that aimed at addressing the network resilience of mutualistic interactions have been mainly based on meta-analyses and numerical simulations such as minimalist process-based and stochastic modelling (Huang and D'Odorico, 2020; Schleuning et al., 2016; Vieira and Almeida-Neto, 2015) of aquatic (Elliott, 2010) and terrestrial ecosystems (Dakos and Bascompte, 2014). However, it still remains unknown to what level ecological fluctuations along climatic gradients would shape the network resilience of mutualistic ecosystems in the future (Ratajczak et al., 2018).

Undisturbed ecosystems are often characterised by functionally diverse plant-pollinator networks and damages within such ecosystems can be buffered to a certain extent (Cardinale et al., 2011). Due to global change, several interacting features are known to influence the network resilience of plant-bee interaction (Kaiser-Bunbury and Blüthgen, 2015). As a consequence, the loss of ecosystem services and functioning due to disrupted plant-pollinator interaction networks may be inevitable if such disturbances persist, and might lead to irreversible changes in such systems (Huang and D'Odorico, 2020).

Functional redundancy and complementarity between mutualists can buffer the effects of declining species within an ecosystem (Kühnel and Blüthgen, 2015), with complementary species-rich ecosystems being more efficient in exploiting resources than species poor ecosystems. Alternatively, redundancy informs on the number of species with similar functional traits providing positive feedback that stabilises and sustains operations within an ecosystem (Cadotte et al., 2011). Ecosystems harbouring larger numbers of such species will undergo little to no effect in the event of a disturbance, unlike less diverse systems, a situation called “insurance effect” (Downing et al., 2012). However, studies aiming at investigating the underlying mechanisms influencing network resilience across different ecosystems are limited (Huang et al., 2021; Nagaishi and Takemoto, 2018; Kaiser-Bunbury et al., 2017) and geographically biased (Archer et al., 2014).

Functional trait diversity is known to unify demographic and functional dissimilarities between co-occurring species relative to processes of coexistence (Tilman, 2004). As such, spatial and temporal complementarity of diverse pollinator communities can increase pollination success and ecosystem services (Hoehn et al., 2008). Therefore, a loss in species diversity for a functional group might indicate weak self-regulating variations of multiple species leading to an unstable ecosystem. Nonetheless, there is a dearth in studies on the challenges influencing network resilience of plant-pollinator interactions networks, even though such studies are important in enhancing our understanding of which functions within an interaction network are at risk (Baho et al., 2017). Thus, decisions with regard to conservation and restoration of ecosystems can be much better informed.

Empirical studies on plant-pollinator networks along environmental gradients can be influential tools to examine the mechanisms challenging network resilience architectures. Mountains have great conservation values because they harbour a variety of endemic species (Rahbek et al., 2019) and can serve as natural laboratories (Sponsler et al., 2022) for investigating evolutionary and physiological patterns of

species distribution. Along elevational gradients, species interactions can be greatly restructured by biotic and abiotic factors over short spatial scales (Maicher et al., 2020). Moreover, seasonal changes in climate can directly or indirectly impact species assemblages (Dzekashu et al., 2022, 2023). Along tropical elevations, seasonality is habitually higher at lowlands. High temperatures and low rainfall can cause temporal drought (Körner, 2007), thus leading to a change or turnover in the type and quantity of available food resource to consumer communities (Dzekashu et al., 2022). Across elevation gradients, changes in physiological performance, fitness, and shifts in the distribution of functional traits of species through sorting and functional trait variation (Siefert and Ritchie, 2016) can influence network resilience in species assemblages and ecosystems in general. Thus, recovery from fluctuating environmental conditions such as those across tropical elevations is vital for the stability and maintenance of tropical mountain ecosystems. Even though tropical mountains are known to hold the most extreme gradients in climate and richness in species (Körner, 2007; Peters et al., 2016a; Peters et al., 2019), contemporary studies addressing the impact of elevation gradients on plant-pollinator network resilience supported by empirically data sets are still lacking (Nagaishi and Takemoto, 2018).

Changes in natural vegetation structures due to human activities such as the fragmentation of natural habitats is also a major driver in declining biodiversity (Aguilar et al., 2006). The configuration of landscapes such that the number, and size at which patches are connected to each other have important contributions on the meta-population dynamics of species within an ecosystem (Hanski and Ovaskainen, 2000; Herrero-Jáuregui et al., 2022). Landscape configuration can isolate populations particularly pollinators, reduce optimal resource intake with higher energy cost associated with long flights between patches and corresponding trade-offs linked to physiological limitations; and in flowering plants through phenological changes, limitations in efficient pollen transfer, reproductive fitness and population viability (Aguilar et al., 2006). Despite the vast number of studies available on this topic, there still exists a lack of evidence backed by empirical datasets showing the influence of landscape configuration or fragmentation on network resilience.

In this study, carried out along two mountain slopes of the Eastern Afromontane Biodiversity Hotspots (EABH) in Kenya, we aimed to understand the network resilience of plant-bee mutualistic interactions. We chose bees as our focal taxa because of their importance in the provisioning of the ecosystem service of pollination (Potts et al., 2003; Steffan-Dewenter and Tschamntke, 2001) and sensitivity to changes in the environment (e.g. changes in climate and flowering plant resources) (Classen et al., 2015; Lasway et al., 2022). To achieve our goals for this study, we first aim to calculate bee and plant network resilience using the single macroscopic network resilience parameter (β_{eff}) (Gao et al., 2016; Nagaishi and Takemoto, 2018) and reveal changes in its patterns along an elevation gradient. This parameter (β_{eff}) is a one-dimensional mathematical model, quantifiable from an ecological network. It defines the state of an ecosystem (for example species extinctions or coexistence) against disturbances such as loss in interactions, species, interaction weight or any combinations therefrom. Second, we evaluate network resilience by the structure of plant-pollinator interaction networks (i.e. modularity, nestedness, link rewiring, and diversity of plants and pollinators), bee functional traits (Classen et al., 2017; Peters et al., 2016b), and landscape fragmentation and climate.

2. Methods

2.1. Study area and time of study

We recorded plant-bee pollinator visitation frequencies along two elevational gradients in the Eastern Afromontane Biodiversity Hotspot (EABH) in Kenya. One elevation gradient spanned from 525 to 1,865 m asl in the Taita Hills, Taita-Taveta county in the coastal region (38°10' to 39°03'E, -3°15' to -4°05'S) and the other along a 1,470 to 2,530 m asl in

Murang'a County, found in the central region ($36^{\circ}43'$ to $37^{\circ}27'E$, $0^{\circ}34'$ to $1^{\circ}55'S$) Fig. 1. These two elevation gradients fall within the same biogeographical unit that extends from the Aberdare ranges to the Taita highlands. The rich biota of the Eastern Arc Mountains, together with the Coastal forest of Tanzania, form the Eastern Arc/Coastal forest biodiversity-rich zones of Kenya and Tanzania (Boitt et al., 2015).

Our study covered the four phenological periods in this region between July 2019 and April 2020 (long dry and cold season: July, short dry and cold season: September–October, short rainy and warm season: November and December, long rainy and warm season: March–April). In total, 50 study plots of sizes $100\text{ m} \times 100\text{ m}$ were set up along the two elevation gradients, with equal distribution (i.e. 25 study plots) per gradient. Study plots were independent from each other and were always positioned such that the geographic distance between adjacent plots ranged from ca. 2.3 to ca. 8.2 km (ensuring that adjacent sites are not within the same foraging range) and ensuring an elevational accretion of ca. 100–250 m between connecting plots (Dzekashu et al., 2022) Fig. 1. All selected plots comprised a high vegetation heterogeneity of mostly regrowth vegetation with substantial floral resource availability for bee visitors. A regrowth vegetation has important implications in landscape heterogeneity and conservation of rare species (Tschamtkke et al. 2011). It is formed as a result of subsistence farming and grazing activities which gradually replaces a natural vegetation and comprises of natural herbs and woody plants, growing and intermixing with single or a small number of large trees (Dzekashu et al., 2022). The lower elevations were characterised by an arid and semi-arid sub-tropical climate, with savannah and shrubland vegetation, while the higher elevations are typified by an intermix of natural and anthropogenic habitats such as; indigenous bushland, pasture and human settlement with subsistence farming activities such as; cucumber (*Cucumis sativus*), beans, mangoes, tomatoes, plantains, bell pepper (*Capsicum anum*),

maize, banana, cabbage, and spinach. The subsistence farms are closely accompanied by sets of large scale agricultural plantations such as sisal (*Agave sisalana*) in Taita, and pineapple, tea (*Camelia sinensis*), coffee and avocado plantations in Murang'a (Dzekashu et al., 2022). The five most species-rich plant families found in these regions and on which bees regularly forage on are the Asteraceae (e.g. *Tithonia* sp., & *Sphaeranthus* sp.), Fabaceae (e.g. *Senna* sp.), Lamiaceae (e.g. *Ocimum* sp., *Lippia* sp., & *Leucas* sp.), Malvaceae (e.g. *Abutilon* sp.) and Poaceae (e.g. *Brachiaria* sp.) (Dzekashu et al., 2022).

The mean annual precipitation increased with elevation with a bimodal seasonal pattern (i.e. short rainy period: November to December and long rainy period: March to May, which are intercepted by a short dry period: January–February and a long dry period: June–October) (Dzekashu et al., 2022) and ranged between $\sim 250\text{ mm}$ to ca. 2000 mm (Orodho, 2006) from lower to higher elevations. The mean annual minimum and maximum temperatures ranged from ~ 17.5 to 19°C and ~ 29 to 31°C (Gebrechorkos et al., 2019). The region is characterised by a high seasonality in temperature and precipitation.

2.2. Plant-pollinator observations

We conducted four standardised sampling rounds between July 2019 and April 2020. This enabled us to cover the four major seasons in these regions. During each sampling, plant-bee interactions were conducted for 2-h per plot, between 09.00 and 17.00. The time range covers the peak period of bee activities. Throughout the entire sampling period, plant-bee observations were piloted by an unchanged team of three experienced observers to avoid sampling bias. A plant-bee interaction (observation) was defined as a contact made by a bee with the reproductive parts of a flower (i.e. anthers or stigma). All bees visiting flowers were collected with the help of standardised sweep nets and an

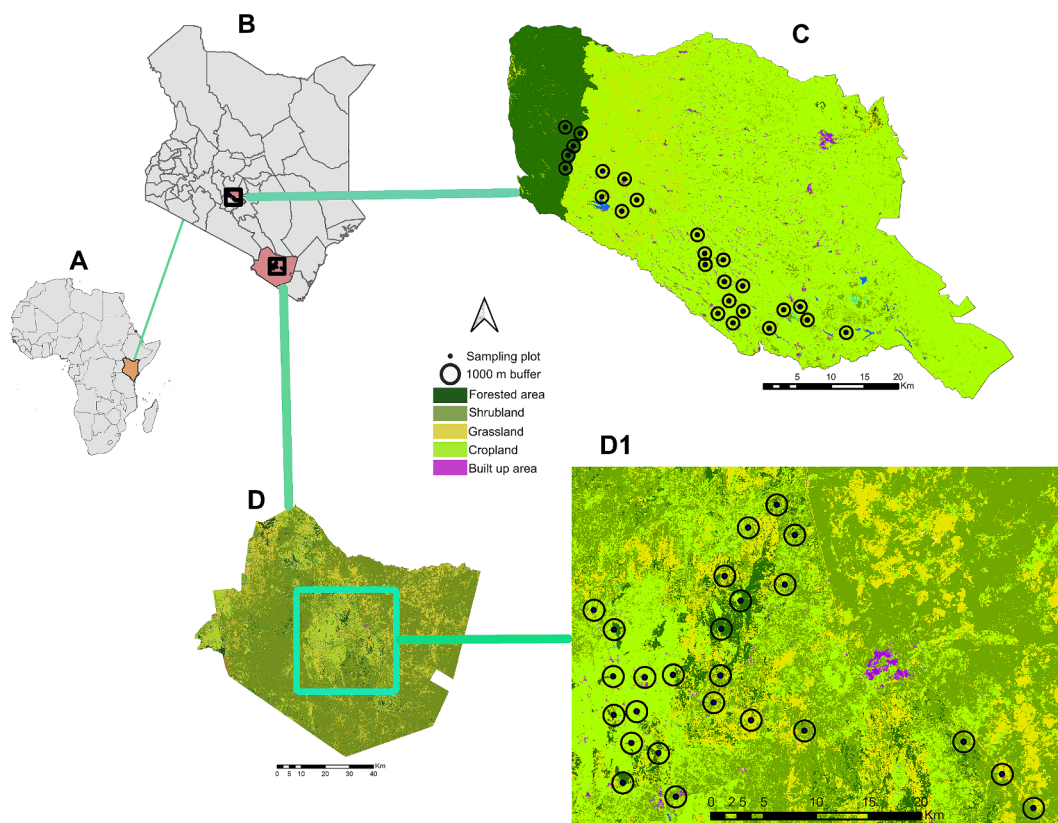


Fig. 1. Map of African continent (A) and the study sites of the two elevation gradients in Kenya (B). Murang'a county (C), Taita Taveta county (D), focal sampling area in Taita Hills (D1). All study plots are positioned along the elevation gradients. Each gradient contains 25 study plots. Circles around plots represents landscape radii buffering (spatial scales of 1000 m) from which the fragmentation index (number of patches) was computed. All layers were clipped from ESA's Sentinel-2 Global Land Cover (<http://seom.esa.int/index.php>) with a 20 m resolution and accuracy for the year 2016.

improved Prokopack aspirator Model 1419 (John W. Hock, Gainesville, Florida, USA) to collect bees on taller plants (trees up to ~4 m high) that were challenging to sample using sweep nets. We ensured all sampling events were conducted when the weather conditions were sunny or dry, rain-free, with no or shallow winds and no fog. We followed a very slow and gentle movement around an entire plot (to prevent disturbances in the vegetation and increase our chances of recording more interactions) and observed flowers for bee visitors (Westphal et al., 2008). We also collected all plants visited by bees and took high-resolution images using a digital camera (Canon EOS Rebel T7 DSLR) for identification. Bees were all identified to genus level and, after that, sorted into either species or morphospecies following Michener (2007) and Eardley et al. (2010), while all plant species were identified to species level. All plant and bee identifications were performed by experienced taxonomists.

2.3. Estimation of plant and bee network resilience indices

High functional redundancy is known to enhance network resilience. It has been shown that network structures with less generalised interactions among mutualistic (here, plant-pollinator) species in a particular system strengthen niche complementarity (Blüthgen and Klein, 2011). Furthermore, such an interaction would reduce the interdependence of interacting species, thereby decreasing network resilience in species loss and functionality in local assemblages (Kaiser-Bunbury and Blüthgen, 2015). From our quantitative plant-bee interaction network data, we estimated the network resilience of plants and bee-pollinators (β_{eff} plants and β_{eff} bees) separately (Eq. (1)) from mutualistic networks per plot (i.e. pooled across the four sampling sessions) as in Gao et al. (2016) and Nagaishi and Takemoto (2018) using the following formula;

$$\beta_{\text{eff}} = \frac{\sum_{ij} A_{ij} A_{ji}}{\sum_{ij} A_{ij}} \quad (1)$$

Here, the matrix A_{ij} relates to the weighted plant-bee network assembled by projecting the quantitative plant-bee interaction networks on the plant-bee data set and is obtained by Eq. (2);

$$A_{ij} = \sum_{k=1}^P \frac{M_{ik} M_{jk}}{\sum_{s=1}^B M_{sk}} \left(A_{ij} = \sum_{k=1}^B \frac{M_{ki} M_{kj}}{\sum_{s=1}^P M_{ks}} \right) \quad (2)$$

Where: A_{ij} indicates plant-bee interaction networks and is defined as the sum of the inverse degrees of mutual partners between plant-bee i and j in the interaction network. Following Gao et al. (2016) and Nagaishi and Takemoto (2018), A_{ij} specifies the weight of the mutualistic interaction between i and j , expressed as the density of mutual interactions between i and j centred on these premises: (i) A stronger interaction frequency is detected between plant-bee i and j when the plant-bee share additional mutual plant-bee k ; (ii) Conversely, the influence to each plant-bee is weaker when bee-plant k interacts with more plant-bee (Nagaishi and Takemoto 2018). M_{ik} is the $B \times P$ matrix of the mutualistic interaction. Here, a mutualistic interaction between a plant i and a bee k occurs and is represented by $M_{ik} = 1$, and a mutualistic interaction is absent when $M_{ik} = 0$.

2.4. Functional diversity (FD)

To characterise the contribution of species functional diversity on network resilience, we calculated the functional dispersion index (FD_{is}) of bee species. This index approximates species dispersion in a multifaceted functional trait space based on principal coordinate analysis (Laliberté and Legendre, 2010). Here, we focused on four bee traits with known effects on ecosystem functioning and stability. That is body size (ITD length), proboscis length, nesting behaviour, and sociality (Marcacci et al., 2022; Osorio-Canadas et al., 2022).

We measured the intertegular distance (ITD) of 176 bee species (i.e. a

total of 2672 bee specimens) as a proxy for bee body size. This process is the most acceptable and has been widely used in evaluating bee body sizes (Osorio-Canadas et al., 2022; Roquer-Beni et al., 2020) as it indicates a high correlation to total dry mass (Cane, 1987). We also conducted measurements of proboscis length (a proxy for their feeding resources) for the same 176 bee species (here, a total of 881 bee specimens), for a minimum of one and a maximum of thirteen specimens per species. We ensured that ITD and proboscis length measurements were conducted only for the same species of bees available (Table S8). Measurements of bee body size (i.e. intertegular distance (ITD)) and proboscis lengths were conducted using a handheld Dino-lite digital microscope (AnMo Electronics Corporation, Hsinchu, Taiwan) powered with a DinoCapture 2.0 software (version 1.5.39.B). All bee species were classified into four nesting categories (ground, cavity, parasitic, and others) and two social levels (social and solitary) following Michener (2007) (but see Marcacci et al. (2022)). To calculate the functional dispersion, we first calculated for each (morpho)species a Gower dissimilarity matrix to estimate the functional distances between species (Gower, 1971), controlling flexibility in qualitative and quantitative traits (ITD length, proboscis length, nesting behaviour, and sociality) using the *gawdis* function calculated with the 'FD' package (Laliberté et al., 2014).

2.5. Climatic variables

Using our plot coordinates, we obtained the following climatic variables for each of our study plots from the Climatologies at High-Resolution for the Earth's Land Surface Area (CHELSA) database: BIO1: mean annual air temperature (MAT), BIO12: mean annual precipitation (MAP). This database is being extensively used in ecological studies. It provides climate data at a 30 arc-seconds (ca. ~1 km²) resolution with more precise precipitation data across elevations compared to other databases (Karger et al., 2017).

2.6. Landscape diversity and fragmentation

Landscape proportions and fragmentation index for the most common land cover types (Forest and tree cover, Grassland, Shrubland, Cropland and Built-up areas) were calculated for each plot. These land cover attributes significantly determine bee diversity and distribution (Millard et al., 2021; Ochungo et al., 2022), impacting the availability of nesting sites and feeding resources (Otto, 2016). We calculated the number of patches as an index of fragmentation because it best elucidates the relationships between ecological processes and habitat fragmentation (Püttker et al., 2020) with important implications in species assemblages (Vega and Küffer, 2021). The fragmentation index and landscape proportions were assessed at a spatial scale of 1,000 m radius around each study plot. This perimeter covers the flight ranges of most tropical bee species (Wikelski et al., 2010). We clipped our layers from ESA's Sentinel-2 Global Land Cover (<http://seom.esa.int/index.php>) with a 20 m resolution and accuracy for 2016. Landscape radii buffering and fragmentation index were computed for each plot using the plugin LecoS 3.0.0 (Jung, 2013) in QGIS 3.10.1 and FRAGSTATS v 4.21 (McGarigal et al., 2002).

2.7. | Network indices

Following Dormann et al., (2021), we quantified our bee-plant interaction network ($B \times P$) for each plot using the whole data set with all interactions in a matrix form. Since we recorded actual visitation preferences by bees on different plant species (focal observation), we used a more robust framework and estimated network indices using weighted data (i.e. weighted by the number of interactions). All network indices were calculated using the 'bipartite' package (Dormann et al., 2021) in the R statistics platform version 4.0.3 (R Development Core Team, 2020). We choose the following indices that best elucidate

extinction risk and stability in the ecosystem:

Weighted Nestedness Overlap and Decreasing Fills (wNODF): It describes community patterns of species assemblages whereby specialist species tend to interact with generalist species (Almeida-Neto et al., 2008). Its values range from 0 to 100, where 0 indicates perfect fully nested networks while 100 indicates a high tendency of specialists to interact with generalists, which interact more with each other (Almeida-Neto and Ulrich, 2011). Nested networks act as buffers against the temporal fluctuation of specialists. We calculated nestedness using the *weighted* NODF (wNODF) algorithm (e.g. Almeida-Neto and Ulrich, 2011).

Modularity (Q): Here, subsets of species (link-rich clusters or sub-communities) interact more among themselves compared to other species in the network, forming a module or compartment (Carstensen et al., 2016; Dehling, 2018). We estimate the modularity values for each plot using the *ComputeModules* algorithm (Dormann et al., 2021). The values in modularity range from 0 (no link-rich clusters) to 1 (total compartmentalisation of species). Modularity increases the stability in plant-pollinator networks by cushioning the effects of perturbations across link-rich clusters (Olesen et al., 2007; Tylianakis et al., 2010; Fletcher et al., 2013; Grilli et al., 2016).

Link rewiring (β_{OS}): It quantifies spatio-temporal dynamics between interaction networks (i.e., dissimilarity due to shared species subwebs) (Poiso et al., 2012; Schwarz et al., 2020; Fründ, 2021; Poiso et al., 2022), providing an in-depth understanding on how the interacting species assemblages respond to global change drivers. The rewiring of broken links is known to increase ecosystem stability (Vizentin-Bugoni et al., 2020). We here, aimed to quantify the impact of seasonal network dynamics on network resilience. Its values range between 0–1. Higher values specify increased variation in seasonal interacting subsets (Caradonna et al., 2017). The *betalink* function (Schwarz et al., 2020; Dormann et al., 2022) was used to estimate the degree of temporal dynamics between seasonal networks (i.e., the cold-dry season and the warm-wet season).

2.8. Statistical analyses

All statistical analyses were performed in R statistics platform version 4.0.3 (R Development Core Team, 2020) using the following packages: 'MuMIn' (Barton, 2009), 'Vegan' (Oksanen et al., 2019), 'mgcv' (Wood, 2006), 'corrplot' (Wei et al., 2017), 'Caret' (Kuhn, 2008), and 'piecewiseSEM' (Lefcheck, 2016).

To determine patterns in network resilience with elevation, we performed a direct comparison of network resilience with elevation using Generalised Additive Models (GAM). GAM was computed using the *gam* function in the 'mgcv' package with a Gaussian type family and an 'identity' link function. GAM uses non-parametric smoothers to pervade simple and complex nonlinear and linear relationships (Wood, 2006). The basis dimensions were set to $k = 5$ to avoid over-parameterisation (Peters et al., 2016).

We calculated bee species diversity (b_v) as the cumulative species richness per study plot across all seasons. To determine plant species diversity (F_v), we followed the same procedure as outlined for the bees above (also see Dzekashu et al., 2022).

We used path analysis (i.e. Structural Equation Models, SEM) to unravel the direct and indirect effects of all independent variables on plant and bee network resilience. Due to a lack of data on some explanatory variables for all 50 study plots, we reduced our dataset to 47 study plots with complete data. We followed a 2-step approach to achieve final structural equation models. First, we used a multimodal inference framework to disentangle the effects of ecological processes influencing network resilience in bee and plant communities. Here, we established and selected for each network resilience index (β_{eff} plants and β_{eff} bees) a set of potential path combinations of predictor variables most likely to delineate changes in the network resilience of plant-bee mutualistic interactions (β_{eff} plants and β_{eff} bees). We examined the

effects of climate (MAT, MAP), interaction networks (modularity (Q), nestedness (wNODF), link rewiring (β_{OS})), community assemblage (floral diversity (F_v), bee diversity (b_v)), landscape fragmentation (number of patches), and bee functional traits (FD) as predictor variables on overall changes in bee and plant network resilience by applying a multimodal inference (ordinary linear models) framework based on the Akaike Information Criterion (AIC). We used the *dredge* function within the 'MuMIn' package and selected all models presenting a $\Delta AIC_C < 3$. To derive support for individual models, we used the Akaike Information Criterion (AIC_C) with second-order biased correction and not the original AIC since our sample size was small when equated to the assessed parameters ($n/K < 40$) (Burnham and Anderson, 2002). All our independent and response variables were standardised by z-transformation to allow an easy comparison of effect sizes among independent variables. We fitted full models for each criterion variable listed above and calculated AIC_C values for these and all nested models. Second, to select the best model path combination for our SEM as represented across the full model space obtained from above, we constructed all possible SEM structures with these models and selected the SEM with the lowest AIC using the *sem* function in the 'piecewiseSEM' package. More so, all variables used in the path analysis were standardised to enable easy comparison of path coefficients by assessing the effect strength of all direct and indirect variables. The goodness-of-fit of our path analysis used to compare support for all pre-selected competitive path model combinations was estimated using four distinct fitness indices; goodness-of-fit Index (GFI), Standardised Root Mean Square Residual (SRMR: good range: a value < 0.08), Comparative Fit Index (CFI: good range: a value > 0.9), and Root-Mean Squared Error of Approximation (RMSEA: good range, values < 0.8) (Hu and Bentler, 1999).

To obtain the most important variables, we set the correlation threshold of explanatory variables to $r > 0.7$ (Dormann et al., 2013) using the *findCorrelation* function in the 'Caret' package. To graphically visualise the collinearity and or hidden patterns among independent variables, we used the *corrplot* function in the 'corrplot' package. We noticed that MAT and MAP were fairly higher correlated than the prescribed threshold (i.e., $r > 0.7$) and could cause glitches in causal inference Fig. S1. However, we proceeded to analyse them together because we were interested in understanding the impact of climate on the network resilience of plant-bee mutualistic interactions in these regions. We further reported the degree of correlation for these and all predictor variables using our multi-model inference framework to descend support for predictor variables Fig. S1. Comparisons between competitive models showed unswerving support for most effects on all variables measured.

3. Results

3.1. Diversity of bees and plant interaction

Across the entire study, we identified 186 bee species and 312 plant species involved in 16,741 unique interactions (Tables S6 & S7).

3.2. Effects of elevation on bees and plant network resilience

Across the studied East African mountains, the network resilience of plants and bees increased non-linearly and significantly with elevation (network resilience bees: $n = 50$, estimated degrees of freedom (e.d.f.) of the smooth term = 1.7, $F = 6.12$, $p < 0.01$, Fig. 2-a; network resilience plants: $n = 50$, e.d.f. = 2.02, $F = 4.3$, $p = 0.02$, Fig. 2-b). Nonetheless, the explained deviance (ED) was relatively low (network resilience bees: ED = 21.7 %, network resilience plants: ED = 19.4 %).

3.3. Drivers of bee and plant network resilience

Climate, bee and plant community diversity, functional traits, landscape fragmentation, and network variables changed across the

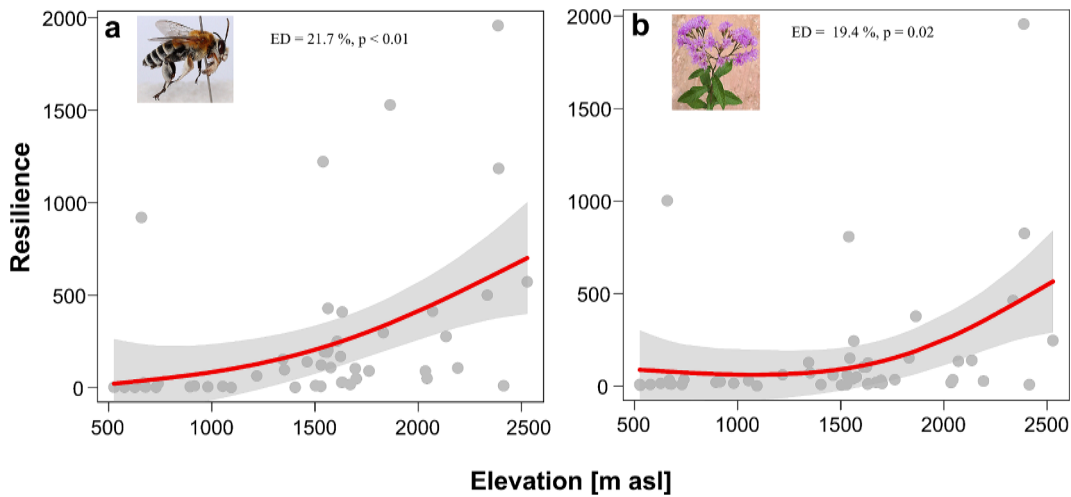


Fig. 2. Patterns of network resilience in bee and plant species with elevation. (a) Patterns of bee network resilience with elevation. High values indicate higher network resilience. (b) Patterns of plant network resilience with elevation. All diversity trends were analysed using generalized additive models (Gaussian family, basis dimension $k = 5$). Dots represent observed values of resilience in bees and plant species per study plot.

elevation gradient Fig. 3 and significantly affected bee and plant network resilience. Still, the type and scale of effects differed between response variables Figs. 4, 5 & 6. We found elevation to be associated

with bee and plant network resilience. However, a combination of climate, bee and plant community diversity, functional traits, landscape fragmentation, and network indices explained a higher level of

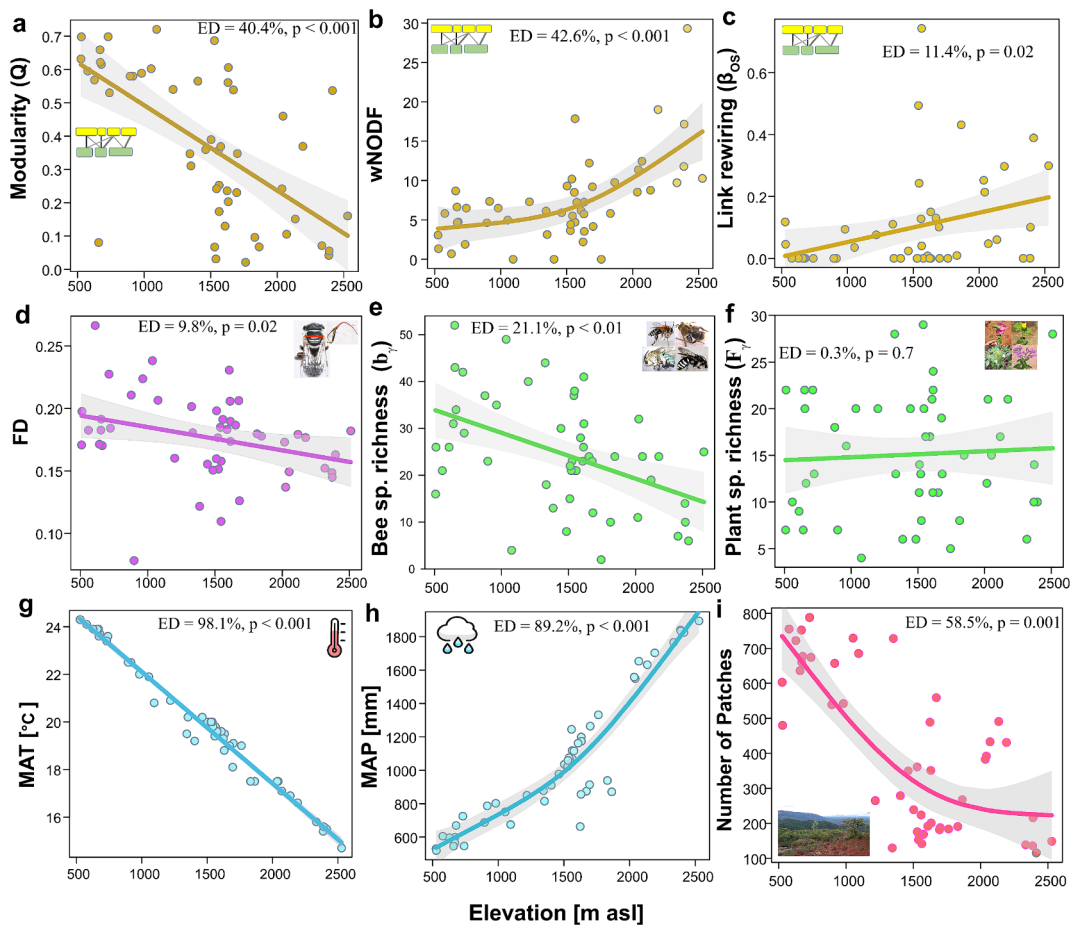


Fig. 3. Patterns of interaction networks (yellow), assemblage diversity (green), functional diversity (purple), climate (blue) and landscape diversity (pink) variables used to explain changes in plant and bee network resilience across the elevation gradient. Patterns of: (a) modularity (Q), (b) weighted nestedness $wNODF$, (c) link rewiring (β_{os}), (d) bee functional dispersion (FD), (e) bee species richness (b_7), (f) plant species richness (F_7), (g) mean annual temperature (MAT), (h) mean annual precipitation (MAP), (i) number of patches (NP). All trends were analysed using generalized additive models (Gaussian family, basis dimension $k = 5$). Dots with different colours represent observed values per study plot. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

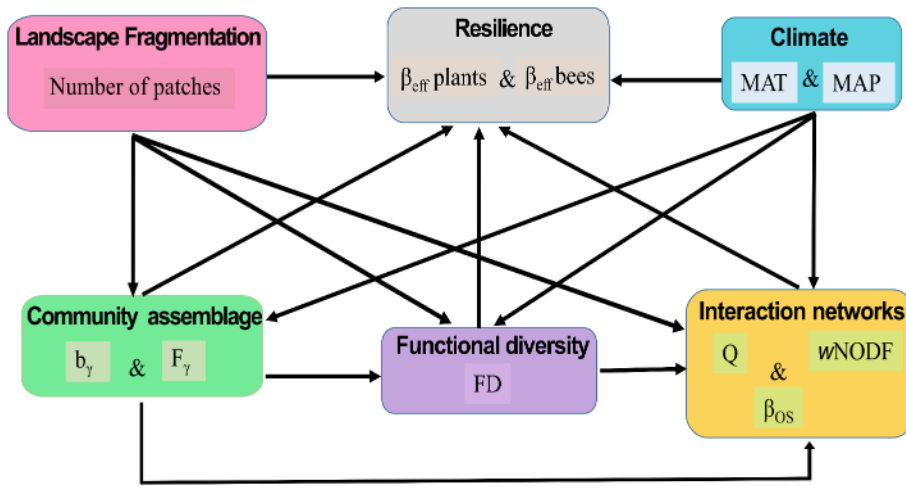


Fig. 4. Conceptual causal pathways of interaction networks (yellow), assemblage diversity (green), functional diversity (purple), climate (blue) and landscape diversity (pink) on plant and bee network resilience. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

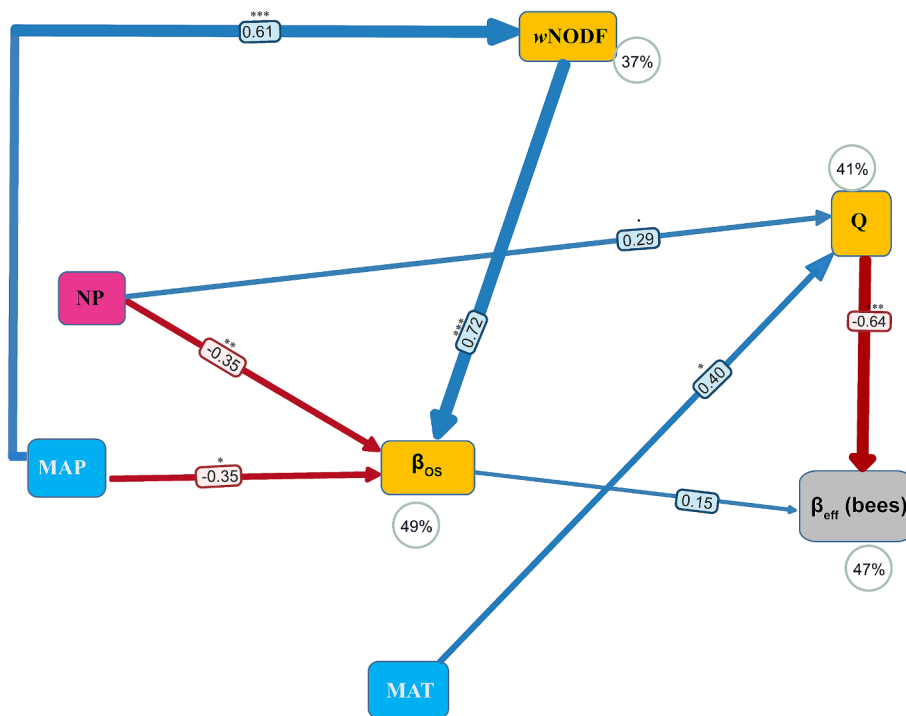


Fig. 5. Structural equation model showing the direct and indirect effects of interaction networks (yellow), climate (blue) and landscape fragmentation (pink) on bee network resilience. Bee network resilience ($\beta_{\text{eff}} \text{ (bees)}$), mean annual temperature (MAT), mean annual precipitation (MAP), number of patches (NP), modularity (Q), weighted nestedness (wNODF), network link-rewiring (β_{os}). Statistical significance is represented by asterisks (*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$). Model goodness-of-fit: GFI=0.94, SRMR=0.046, p-value = 0.80, indicating good support for the model. Numbers within arrows show the standardised path coefficients. Size of arrow indicates the magnitude of the effect. Red and blue arrows denote negative and positive effects respectively. Percentage values represent the explained variance of endogenous variables (response variables). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

differences in network resilience. The structural equation model for bee ($\beta_{\text{eff}} \text{ bees}$) and plant ($\beta_{\text{eff}} \text{ plants}$) network resilience tuned well to the data ($\beta_{\text{eff}} \text{ bees}$: goodness-of-fit Index (GFI) = 0.951, Standardised Root Mean Square Residual (SRMR) = 0.056, Comparative Fit Index (CFI) = 1, and Root-Mean Squared Error of Approximation (RMSEA) = 0.00, $p = 0.865$; $\beta_{\text{eff}} \text{ plants}$: GFI = 0.965, SRMR = 0.046, CFI = 1, and RMSEA = 0.00, $p = 0.894$), explaining 47% and 39% of the total variation in bee and plant network resilience respectively (Figs. 5–6, Tables S4–S5).

3.3.1. Effect of climate on network resilience of bees and plants

Climate had an indirect association with bee network resilience ($\beta_{\text{eff}} \text{ bees}$). MAP negatively influenced the temporal dynamics between seasonal networks (β_{os}), which in turn positively but non-significantly influenced bee network resilience with a standardised path coefficient of -0.05 ($[-0.35] \times 0.15$, Fig. 5), while MAT had a positive effect on bee network resilience via a positive impact on network modularity, which in turn negatively and strongly influenced $\beta_{\text{eff}} \text{ bees}$ (path coefficient = -0.3 , i.e. $(0.40 \times [-0.64]$, Fig. 5). On the other hand, climate

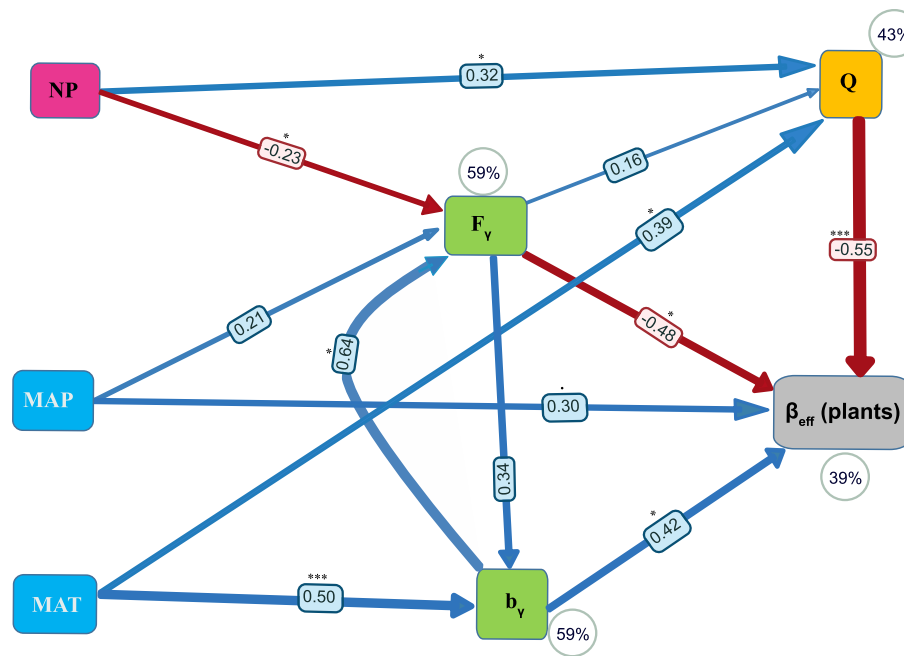


Fig. 6. Structural equation model showing the direct and indirect effects of interaction networks (yellow), plant and bee species diversity (green), climate (blue) and landscape fragmentation (pink) on plant network resilience. Plant network resilience (β_{eff} (plants)), plant species richness (F_{γ}), bee species richness (b_{γ}), mean annual temperature (MAT), mean annual precipitation (MAP), Number of patches (NP), modularity (Q). Statistical significance is represented by asterisks (*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$). Model goodness-of-fit: GFI=0.93, SRMR=0.052, p -value = 0.56, indicating good support for the model. Numbers within arrows show the standardised path coefficients. Size of arrow indicates the magnitude of the effect. Red and blue arrows denote negative and positive effects respectively. Percentage values represent the explained variance of independent variables (endogenous variables). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

had both direct and indirect effects on plant network resilience (β_{eff} plants) through several pathways Fig. 6: one directly from MAP to β_{eff} plants (path coefficient = 0.3, $p = 0.07$) and two indirectly from MAP-mediated by network modularity and plant (F_{γ}) species diversity Fig. 6. One pathway indirectly and positively from MAT via b_{γ} species diversity (path coefficient = 0.2, i.e. 0.50×0.35) and three indirect pathways from MAT mediated by network modularity, bee (b_{γ}) and plant (F_{γ}) species diversity Fig. 6. Including MAP in the models significantly improved the proportion of explained variance (R^2) in β_{eff} plants (Table S5).

3.3.2. Effect of compositional diversity on bee and plant network resilience

We found that plant species (F_{γ}) diversity was directly and indirectly related to β_{eff} plants. One direct and significant pathway from F_{γ} to β_{eff} plants (path coefficient = -0.47 , $p = 0.01$, Fig. 6), two indirect pathways from F_{γ} mediated by network modularity (path coefficient = -0.09 i.e., $0.16 \times [-0.55]$) and bee species diversity (path coefficient = 0.14 i.e., 0.34×0.42). We also found that bee species diversity (b_{γ}) had a direct and positive influence on overall β_{eff} plants (path coefficient = 0.42 , $p = 0.01$; Fig. 6, Table S5).

3.3.3. | Effect of functional trait diversity on bee and plant network resilience

We found that the relationship between bee functional trait diversity (FD) and bee-plant network resilience was positive but non-significant (β_{eff} bees: path coefficient = 0.08 , $p = 0.48$; β_{eff} plants: path coefficient = 0.10 , $p = 0.43$; Tables S4 & S5), even though diversity in bee functional traits decreased marginally along the elevation gradient (ED=9.8 %, $p = 0.02$, Fig. 3-d).

3.3.4. Effect of interaction networks on network resilience of bees and plants

We noticed that both bee and plant network resilience were strongly and negatively associated (path coefficient = -0.64 , $p < 0.001$ and $r =$

-0.55 , $p < 0.001$) with network modularity (Figs. 5 & 6; Tables S4 & S5). Additionally, bee network resilience was positive in areas of increasing interaction reassembly (i.e. link-rewiring (β_{OS})), while network link-rewiring increased with elevation (ED=11.8 %, $p = 0.02$; Fig. 3-c). However, it did not reveal any significant influence on β_{eff} bees (path coefficient = 0.15 , $p = 0.2$; Fig. 5, Table S4). More so, bee network resilience increased in areas where specialist species were more inclined to interact with generalists, which in turn interacted more among each other (nested) via an indirect pathway mediated by temporal changes of seasonal networks (β_{OS}), (path coefficient = 0.11 , i.e. 0.72×0.15 ; Fig. 5, Table S4).

3.3.5. Effect of landscape configuration on bee and plant network resilience

Landscape configuration or fragmentation (number of patches, NP) indirectly influenced β_{eff} bees and β_{eff} plants via several pathways. Two of these associations with β_{eff} bees were indirectly mediated by network modularity (Q) and link-rewiring (β_{OS}) (path coefficient = -0.2 , i.e. $0.29 \times [-0.64]$ and path coefficient = 0.04 , i.e. 0.29×0.15 respectively; Fig. 5, Table S4). More so, NP had an indirect association with β_{eff} plants via Q (path coefficient = -0.2 , i.e. $0.32 \times [-0.55]$) and several indirect effects on β_{eff} plants mediated by b_{γ} and F_{γ} via several pathways Fig. 6, Table S5.

4. Discussion

In this study, we found that across the studied East-African tropical montane ecosystems, network resilience in both bees and plants significantly increased with elevation. We unravelled the effects of climate, assemblage diversity, bee functional traits network parameters, and landscape configuration on bee and plant network resilience.

4.1. Elevational and climatic drivers of bee and plant network resilience patterns

From the inception of the idea of species elevational ranges more than a century ago (von Humboldt 1884), the ideal advantage of elevation gradients has been to understand the eco-evolutionary dynamics of animal and plant species and their adaptation to environmental changes (Körner, 2007). In our study, we observed an increasing trend in bee and plant network resilience with elevation. While bee network resilience increased linearly across the elevational strata, plant network resilience increased exponentially from ~1500 m and higher. This means that bee and plant assemblages are well adapted to ecological inconsistencies within certain limits across the elevation gradient. Moreover, the observed network resilience across the elevation gradient can be crucial in offsetting the negative impacts of more frequent environmental perturbations at higher elevations. These findings therefore complement results from previous studies revealing that ecosystem stability is more pronounced across stable systems that can effectively buffer against change drivers (Martin and Watson, 2016).

Furthermore, our results showed that, along the elevation gradient, bee and plant network resilience were influenced by climate. Mean annual precipitation (MAP) had an indirect effect on bee network resilience via link-rewiring as shown by our path model. On the other hand, MAP had a direct positive influence on plant network resilience. Even though the effects of global change on an ecosystem are contingent on the inherent aptitude of the ecosystem to resist or adapt to climate perturbations (Li et al., 2018), these findings point to the fact that species survival hinges on the tenacity of suitable climatic conditions (Loarie et al., 2009). More so, climate change is a known driver of global ecosystems, however, recent studies on some systems suggest some level of network resilience to climatic influence, with many species developing the ability to limit the ever-increasing impacts of climate change (Scheffers et al., 2016). This is true when considering the distribution of many tree species around the Mediterranean basin (Battlori et al., 2020; Hackett-Pain and Friend, 2017). Temperature and rainfall vary across this elevation gradient such that as MAT decreases, MAP increases (Dzekashu et al., 2022). Thus, an interplay between these environmental conditions can restrain trait variations and functional convergence in bee and plant species (Li et al., 2018; Wiczyński et al., 2019). At the same time, species across the elevation gradient of this region often turn to shift their distributions in different seasons towards higher elevations in search of more conducive climatic conditions (Dzekashu et al., 2022).

The positive relationship between rainfall (MAP) and plant network resilience in our study supports the water availability hypothesis. Here, increased rainfall would lead to increased physiological development, hydraulic conductance, inter- and intra-annual growth patterns and population density of plants (Toledo et al., 2011). On the other hand, rainfall negatively influenced network link-rewiring. These adverse effects of predicted increased rainfall can be attributed to the fact that rains hinder flight performance in bees (Samways et al., 2020); hence, they prefer areas with less rainfall (Perillo et al., 2021). Our results further revealed temperature (MAT) to be an important indirect predictor of plant and bee network resilience. As a driver in the diversity and distribution of bee and plant species, it influences ambient conditions (Classen et al., 2015; Peters et al., 2019). In bees, it dictates thermoregulation, metabolic and foraging activity (Osorio-Canadas et al., 2016), while in plants, it regulates mineralisation and adaptation by controlling photosynthesis, nutrient uptake, growth rates, and metabolism (Hoch and Körner, 2012). We can thus argue that across the highlands of Murang'a and Taita, bee and plant species have developed the ability to cope with more stressful environmental conditions. Per se, they have developed high network resilience, which may have helped reduce the effects of climate change on them (Sundqvist et al., 2013; Whittaker, 1956). Hence, different bee and plant species across the elevation gradient retain functional traits that can better select for thermoregulatory and nutrient constraints, thus becoming more

resilient to changing climates (Nadeau et al., 2017; Sundqvist et al., 2011). The effects of changing climate due to alternation in the interaction of temperature and precipitation has led to solid seasonality across relatively short distances along the topo-geography. This alternation of climate has equally been identified as an important driver of leaf production, photosynthesis and radial growth in some Mediterranean plant species (Gavinet et al., 2019; Misson et al., 2010) as well as in the diversity of tropical bee communities (Dzekashu et al., 2022). Even though plant species at the lower elevations of the eastern Afromontane biodiversity hotspot do encounter severe drought conditions during the dry seasons, the majority of the bee species shuffle between elevational ranges under such fluctuating climatic conditions (Mayr et al., 2021a,b; Dzekashu et al., 2022).

4.2. Influence of assemblage diversity and bee functional traits

Our results revealed that network resilience is best retained by bee and plant species diversity. Species diversity is a known contributor in ecosystem stability, invasibility, and productivity (Tilman et al., 2014). Previous studies along these elevation gradients showed a high density of beekeeping activities by local indigenes in the forested highlands (Dzekashu et al., 2023). This indicates that, an accumulation of functionally abundant species may help recover ecosystem functioning (Le Bagousse-Pinguet et al., 2021). Moreover, bee abundance increases seed set in most plant species (Greenleaf and Kremen, 2006). These findings are similar to those of other studies (Corcos et al., 2020; Rogers et al., 2014), which found that a high abundance of bees, especially the super-generalist honeybee, contribute to network stability and network resilience since they can utilise several plant species. This visitation frequency would, in turn, have a positive effect on plant reproduction and network resilience via pollination success (Rogers et al., 2014), as only a few plant species might not be pollinated. In case of species extinction, plant functional groups become more robust in case of loss in any flower visitors (Corcos et al., 2020).

We also found plant species diversity to be an important contributor to plant network resilience. The robust and negative relationship between plant species diversity and network resilience may therefore imply that, plant communities at high elevations with a known prevalence of increased season length (Rahbek et al., 2019) may prolong the growth period, providing temporal stability that would eventually render the system more resolute to perturbations (Oehri et al., 2017). Also, the reaction of plants to environmental changes (e.g. temperature) is slower when compared to other mobile terrene insects (Kerner et al., 2023; Vitasse et al., 2021).

Previous studies have illustrated unidirectional elevational responses for bee diversity in this region (Dzekashu et al., 2022). Here, the phenology and activity patterns of some bee species are restricted in the cold-dry seasons. In contrast, the activity patterns of others increase in the warm-wetter seasons across the different strata of the gradient (Dzekashu et al., 2022), giving rise to high diversity in bee communities dominated by functionally different species. As such, the lower elevations in this area are more diverse than higher elevations, supporting the idea that warm habitats facilitate species richness in ectotherms (Classen et al., 2015), with higher interspecific competitions during resource-rich seasons (warm-wet). Therefore, as climatic conditions and interspecific interactions modulate species diversity trends, these fluctuating bee diversity patterns may influence plant reproductive success and pollinator efficiency, thus affecting network resilience.

The competitive interactions between bee species might be an important factor restricting the elevational occupancy of several plant species, hence reducing plant network resilience at lower elevations. This, could also indicate that plant assemblages at higher elevations, together with their related ecosystem functions, might not sustain a substantial number of bee species.

Functional diversity is considered a central component and a fitness advantage with important functions in determining resource utilisation

and foraging ranges in bees (Rabelo et al., 2015). Therefore, the influence of bee functional dynamics across the elevation gradient may play a part in driving reproductive success in low-land plant communities. As such, the effects of large body-sized bees are reduced at low elevations due to high plant diversity. Again, large sizes are often attributed to specialists' bees interacting with relatively small or restricted numbers of partnered plant species (Raiol et al., 2021). Since the degree of evolutionary influences such as phenotypic complementarity between interacting partner species largely dictates interspecific interactions (Peralta et al., 2020; Raiol et al., 2021), seasonal substitution of generalist bees by specialist species at higher elevations may have contributed to the observed positive relationship on bee and plant network resilience.

4.3. Impact of interaction networks and landscape configuration

We found that network modularity significantly and negatively correlated with ecosystem network resilience, while network nestedness and link-rewiring exhibited a positive influence on bee network resilience. These findings suggest that, as species adaptation to different interacting partners at higher elevations persists, it will lead to decreased network specialisation (Classen et al., 2020), such that, the majority of specialists found at higher elevations form fewer link-rich clusters with subsets of generalists occurring in the highlands and around where most of the interactions are concentrated. Therefore, the loss of a specialist bee within the interaction may further result in a reduction in network resilience and swifter species extinction cascade since they would lack alternative efficient mutualists to reduce the extinction pressures (Aizen et al., 2012). Interaction network processes introduced drastic changes in network resilience characterised by non-random loss of plant and bee species along the elevation gradient, leading to changes in plant and bee network resilience. A loss of interaction in a mutualistic network may limit the availability of floral resources and effective transfer of pollen, thus threatening plant reproductive success and bee functional fitness (Dixon, 2009; Müller et al., 2006). Our results showed that the sub-networks within a network's levels were well conserved across the elevation gradient with constrained species interactions at higher elevations, thus revealing important implications in the spatio-temporal distribution of local species interactions (Vázquez et al., 2009) and network resilience. This can be complimentary and or redundant at different levels of interactions (Mello et al., 2011) with convergent traits (Carstensen et al., 2016). Our findings further suggest that future reductions in plant and bee species due to low interaction frequency would reduce the chances of such a system to buffer against cascading effects (Simmons et al., 2020). These structural changes along the elevation gradient can be partly explained by link-rewiring (Schwarz et al., 2020), wherein fewer links may be realised among subsets of interacting species over space and time. Even though high generalisation can lead to increased network strength between mutualists (Maia et al., 2021), reduced species diversity at higher elevations may result in low functional redundancy in the mutualistic interactions. A lack of alternate interacting partners may further amplify species extinction (Aizen et al., 2012). The importance of our empirical datasets with regards to seasonal changes in species interaction networks proved vital in understanding interaction flexibility and species assemblage responses to the temporal dynamics between interaction networks and their influence on network resilience (Poisot et al., 2015). It is worth mentioning that other, non-measured factors might equally play a role in the ecosystem stability of this region, since species live in other networks such as prey, predators, and competitors, which would still encounter disturbances that could be of either natural or human influences (Macedougall et al., 2013; Tilman et al., 2012). Moreover, continuous assessment of network topologies over several seasons and years to identify and guide against ecosystem changes, since ecological processes can be greatly affected by inter-annual variation as a result of climate change and other man-made (anthropogenic) activities. Under

such conditions, seasonal trends may have an inter-annual variation, hence a multi-year study will reveal a more detailed picture of network resilience in bees and plants assemblages under global change on mountains in the EABH.

We found that, changes in landscape configuration (fragmentation) had an indirect effect on network resilience via modifications of interaction network properties and quality of flowering resources for bee species. Our results also showed that NP increased the likelihood of subsets of species link-rich clusters interacting more among themselves through the formation of several patchy compartments. A plausible explanation could be that, plant assemblages within fragments in this region are fully established and hardly die out with year-round floral resources, thus attracting and maintaining visits from groups of relatively constant bee visitors. On the other hand, NP reduces the eventual formation of seasonal networks and flower assemblages in highly fragmented areas along the elevation gradient, supporting results from previous studies emphasising the sensitivity of biodiversity along tropical elevation gradients due to human land-use influences (Classen et al., 2015; Gebert et al., 2019; Peters et al., 2019). Interestingly, our results show that interacting species across seasons were able to moderate the cascading effect of NP on bee network resilience through the re-establishment of lost interactions across seasons.

5. | Conclusion

Our findings allow for the evaluation of plant-bee interaction network resilience responses to ecological disturbances across an elevation gradient of the Eastern Afrotropical Biodiversity Hotspot (EABH). We noticed that climate and landscape configurations directly or indirectly influenced network resilience of plants and bees via the modulations of community assemblages and interaction networks. Our results show that, network resilience was lowest at lower elevations. More so, increasing temperatures positively influenced interaction networks and community assemblages of plants and bees. We also found that precipitation had a direct positive effect on plant growth and network resilience, while the fragmentation of habitats negatively influenced plant communities but increased network modularity. Thus, changes in temperature and precipitation on flower resources can dictate trends in bee assemblages leading to noticeable increases in species turnover. This could in turn buffer bees and plants against ecological perturbations along the elevation gradient. In light of the ever-increasing impact of climate change, habitat loss and isolation on biodiversity, it is clear that the fate of bees and plants in this region hinges on some very few supporting factors that are under constant pressure. We therefore suggest that recommendations geared at supporting management efforts should aim at consolidating landscape structures and vegetative heterogeneity. More so, restoration efforts should focus on reducing the effects of climate change and harnessing the survival and persistence of plants and their mutualists' bee visitors in order to restore broken links and improve network resilience and functioning on East African mountains.

CRediT authorship contribution statement

Fairo F. Dzekashu: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Abdullahi A. Yusuf:** Writing – review & editing, Validation, Supervision, Resources, Methodology, Investigation, Conceptualization. **Kazuhiro Takemoto:** Writing – review & editing, Validation, Methodology, Investigation, Formal analysis, Resources, Funding, Conceptualisation, Visualisation. **Marcell K. Peters:** Writing – review & editing, Validation, Supervision, Resources, Methodology, Investigation, Formal analysis, Conceptualization. **H. Michael G. Lattorff:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Ingolf Steffan-**

Dewenter: Writing – review & editing, Visualization, Validation, Supervision, Resources, Methodology, Investigation, Conceptualization.
Christian W.W. Pirk: Writing – review & editing, Visualization, Validation, Supervision, Resources, Methodology, Investigation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All data supporting this study are available from Figshare: <https://figshare.com/s/9f40ef50e99f84ab6e93>.

Acknowledgements

We gratefully acknowledge the financial support for this research by the following organizations and agencies: JRS Biodiversity Foundation (grant number: 60610); the Swedish International Development Cooperation Agency (Sida); the Swiss Agency for Development and Cooperation (SDC); the Australian Centre for International Agricultural Research (ACIAR); the Norwegian Agency for Development Cooperation (Norad); the Federal Democratic Republic of Ethiopia, the Government of the Republic of Kenya; the South African National Research Foundation funding for Rated researchers to AAY and CWWP; and the Kyushu Institute of Technology (Japan) operational support funds to Kazuhiro Takemoto. Fairu Dzekashu was supported by a German Academic Exchange Services (DAAD) funded Ph. D. scholarship in the framework of the African Regional Postgraduate Programme in Insect Science (ARPPIS) and a PG tuition bursary from the University of Pretoria. The views expressed herein do not necessarily reflect the official opinion of the donors. We thank Jayne Macharia and Kennedy Matheka from the National Museums of Kenya (NMK) for bee and plant identifications respectively. We thank Emily Kimathi for help with developing the map of the study sites. We also thank Ritter Guimapi, Frank Ndjomatchoua and Natasha de Manincor for their advice, interesting discussion sessions and ideas on interaction networks and resilience. We are equally very grateful to Kimani James Kinuthia, Ephantus Kimani, James N. Kimani, Kika Junior, Benson Mwakachola, Darius Mwambala, and Mwadime Mjomba for their assistance in the various stages of field work.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2024.112415>.

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