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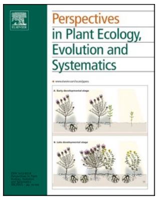

Temporal variability in native plant composition clouds impact of increasing non-native richness along elevational gradients in Tenerife

Meike Buhaly [a,b,*], Amanda Ratier Backes [b], José Ramón Arévalo [c], Sylvia Haider [a]

[a] Institute of Ecology, Leuphana University of Lüneburg, Lüneburg, Germany
[b] Institute of Biology/Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Halle (Saale), Germany
[c] Department of Botany, Ecology and Plant Physiology, University of La Laguna, La Laguna, Tenerife, Spain

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ABSTRACT

Introductions of non-native plant species and their rates of expansion into novel environments are rapidly climbing, and their impact on recipient community composition is currently not well documented. Under the influence of rapidly intensifying human activity, pathways such as roads support such range expansions, especially in vulnerable mountain regions. Using species composition and abundance data collected in disturbed and natural habitats along three mountain roads covering almost 2500 m in elevation, we investigate how non-native plant species impact temporal change in community composition and spatial community dissimilarity on the island of Tenerife over 14 years. We found that, within communities, the number of both native and non-native species increased over time in disturbed habitats, while non-native species richness decreased in natural habitats. While species composition of communities changed over time, this change was not greater with or without non-native species, though any signal of non-native species' influence was likely lost due to the surprisingly high variability in the native community. In disturbed roadside habitats, turnover of species over time played a larger role in temporal change in community composition than changes in species' abundances. Despite increases in richness and occurrences along the elevation gradient, non-native species did not spatially homogenize communities. Although impacts of non-native species on temporal changes in community dissimilarity were presently not found, increases in the number of non-native species and their occurrences illustrate the need for long-term monitoring of altitudinal spread in mountain plant communities, especially in anthropogenically disturbed habitats.

1. Introduction

The extent and rate of spread of plant species outside their native range, especially in the last 50 years, has steadily climbed (Seebens et al., 2017; Van Kleunen et al., 2015). This redistribution of so-called non-native species has often been shown to influence species composition and native species richness of the recipient communities (Kuebbing and Nuñez., 2016; Molinari and D'Antonio, 2014; Lanta et al., 2013; Pearse et al., 2019). A global assessment on the impact of invasive species, i.e. non-native species with strong negative impacts, suggested that overall, resident populations diminished in native species abundance and diversity (Vilà et al., 2011). The spread of non-native species across the landscape can lead to plant communities becoming more similar to each other with regard to their species composition. This process has been described as a loss of beta-diversity or as the homogenization of plant communities (Olden and Rooney, 2006), both terms referring to a loss of floristic uniqueness across space.

Islands have been found to be highly susceptible to plant species establishment and hold disproportionally large populations of non-native species compared to mainlands (Rojas-Sandoval and Acevedo-Rodríguez, 2015; Kueffer et al., 2010; Lonsdale, 1999). A comprehensive analysis examining 30 island groups determined that 50 % of the 383 recorded non-native plant species were considered dominant or co-dominant in a habitat in at least one study island (Kueffer et al., 2010). However, Vilà et al. (2011) found that the impacts of non-native species, despite their large species pools, were not particularly stronger on islands compared to mainlands.

Non-native species are often introduced into new regions due to the transportation of goods, the introduction of ornamental species, and more frequent global travel (Frenot et al., 2001; Kueffer et al., 2010;

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* Corresponding author at: Institute of Ecology, Leuphana University of Lüneburg, Lüneburg, Germany.
E-mail address: meike.buhaly@leuphana.de (M. Buhaly).

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Seebens et al., 2015). Human disturbance is a key factor in non-native species establishment beyond historic ranges, which has become exceedingly common in the last 200 years, and can extend their distributions past the point of initial introduction (Dimitrakopoulos et al., 2022; Mortensen et al., 2009; Seebens et al., 2017; Wohlwend et al., 2021). Newly developed roads offer non-native species an opportunity to spread to regions previously uninhabited by them (Haider et al., 2018; Lembrechts et al., 2017; Mortensen et al., 2009). The intensity of disturbance along roadsides provides constant fluctuations in abiotic conditions, creating pockets of free space for new species to inhabit. Roadsides have been demonstrated to harbor significantly more non-native species than natural environments and provide corridors for spread into the surrounding landscape (Haider et al., 2018; McDougall et al., 2018; Mortensen et al., 2009; Sandoval et al., 2022). A study on the dispersal of common ragweed along freeways in Germany reported that dispersal by traffic spreads propagules an order of magnitude further than primary dispersal (Lemke et al., 2019).

So far, few studies have compared the impact of non-native species on plant communities over time and space in conjunction with human disturbance (Arévalo et al., 2010; Dimitrakopoulos et al., 2022; Fuentes-Lillo et al., 2021; Hejda et al., 2009) due to the need for standardized sampling in permanently marked sites. Investigating the role non-native species play in shifts in community composition provides valuable insight into how these communities may look in the future and how native and non-native species are affected by intensifying anthropogenic activities.

For analyzing non-native species spread, mountains represent an exceptional study location because, in many regions, non-native species are currently restricted to the lowest one-third of the elevational range and non-native richness steeply declines as elevation increases (Alexander et al., 2016; Guo et al., 2018; Haider et al., 2018; Marini et al., 2013). Their relatively pristine environment allows us to clearly see the influence of human disturbance on non-native species distributions and communities. High elevations have remained primarily uninvaded due to the introduction of non-native species in lowlands, though recent evidence suggests that some are now expanding into high alpine regions (Alexander et al., 2016; Haider et al., 2010; Iseli et al., 2023). As human disturbance escalates and residence time of non-natives increases, species can reach further along the elevation gradient and expand well past their introduction in the lowlands (Dainese et al., 2017; Essl et al., 2019; Iseli et al., 2023; Pauchard et al., 2009).

The goal of this study is to better understand how non-native plant species influence changes in community composition over time and space along elevation gradients on the island of Tenerife, and how these changes differ between disturbed and natural habitats. The island of Tenerife currently possesses a large number of non-native species, with many derived from Neoptropical regions, though relatively few are considered invasive (Fernández-Palacios et al., 2023; Morente-López et al., 2023). While studies suggest that the Canary Islands have thus far been resistant to impactful invasion (Fernández-Palacios et al., 2023), it is worth stepping outside the bounds of species lists to quantify the impacts of non-native species at the plant community level. To accomplish this, we use two vegetation surveys collected by the Mountain Invasion Research Network, from 2008 and 2022, with plot pairs in disturbed and natural habitats, evenly spread along three gradients spanning in total 2300 m in elevation. We hypothesize (1 A) that non-native species richness increased over time, predominantly at mid-elevations, due to an established peak in lowlands and the upwards movement of non-native species. Assuming that non-native species richness is higher in disturbed habitats than in natural habitats, this hump-shaped pattern is expected to be more pronounced in disturbed habitats. In contrast, (1B) we do not expect temporal changes in native species richness in any environment. Reflecting these opposing assumptions for native and non-native species, we further hypothesize (2) that the temporal change in community composition is driven by non-native species, and hence more pronounced at mid-elevations as well as in disturbed habitats. Finally, we hypothesize (3) that non-native species are homogenizing plant communities across space. The homogenization effect of non-native species is expected to be strongest in disturbed habitats and in the later study year where non-native species communities are richer and are likely to have spread over time.

2. Methods

2.1. Study area

This study was conducted on the island of Tenerife (28.28°N, 16.15W), the largest island, at approximately 2000 km^2, of the Canary Islands archipelago off the coast of northeast Africa. A prominent feature of the island is the Pico del Teide, a volcano reaching 3718 m a.s.l. at its peak. The Teide divides the island into two distinct climatic regions: a moist north and a dry, arid south (Fernández-Palacios, 1992). Our study sites were located in the south, with mean annual temperatures of 21 ℃ and annual precipitation of 130 mm at sea level (28.040678 N, −16.548512 W), 14.3 ℃ and 500 mm at 1500 m a.s.l (28.177433 N, −16.643417 W), and 9.8 ℃ and below 300 mm at 2300 m a.s.l. (28.254287 N, −16.621682 W) (Arévalo et al., 2005).

The elevation gradient in the south from the coast to the crater of the Teide covers distinct vegetation zones. From the coastline to approximately 1000 m a.s.l., the terrain is dominated by coastal and thermophilous scrub with *Kleinia neriifolia* and *Euphorbia lamarkii* as characteristic species. Further along the gradient is moderately dense forest of *Pinus canariensis* with limited understory of predominantly *Adenocarpus viscosus* and various species of *Sonchus* up to 2000 m a.s.l. From 2000 to 2500 m a.s.l., there are shrub communities dominated by *Descurainia bourgaeana* and *Spartocytisus supranubius*.

2.2. Vegetation surveys

Vegetation surveys were conducted using the Mountain Invasion Research Network (MIREN) framework (Haider et al., 2022). This framework relies on a standardized protocol of vegetation relevés along elevation gradients on mountains, which was established in Tenerife in 2008 (Arévalo et al., 2010). Vegetation was sampled in permanent plots in 2008 and 2022 along three mountain roads with the lowest plot at 24 m a.s.l. and the highest at 2377 m a.s.l. All roads are paved, open year-round, and subject to moderate to high traffic, decreasing with elevation. For each road, 20 sampling sites were selected along the elevation gradient. Two 50 m x 2 m plots were established at each sample site, a roadside plot and an interior plot (hereafter "disturbed" and "natural"). Disturbed plots were situated with the 50 m side of the plot parallel and directly adjacent to the road. Natural plots were located perpendicular to the road with the 2 m edge of the plot 50 m away from the disturbed plot (Fig. 1). In total, 103 of the possible 111 plots were measured in both years, 2008 and 2022. Some plots could not be initially established or, in the later year, reestablished due to private property, construction work, or extreme terrain.

In each plot, we recorded all species and assigned them to three abundance classes: 1 = species with few individuals; 2 = species with at least 10 individuals; 3 = species with at least 100 individuals. These abundance classes were converted into approximate value classes (class 1: one individual, class 2: ten individuals, class 3: 100 individuals) for the analysis. All species were given a native or non-native status determined by the Gobierno de Canarias Banco de Datos de Biodiversidad de Canarias (www.biodiversidad canarias.es\biota; 18/02/2024) and 'Lista da especies silvestres de Canarias' (Acebes Ginovés, 2010) with additional references from other previously published studies in Tenerife (Arévalo et al., 2005; Haider et al., 2010). Taxonomic nomenclature in this study follows World Flora Online (WFO, 2024).

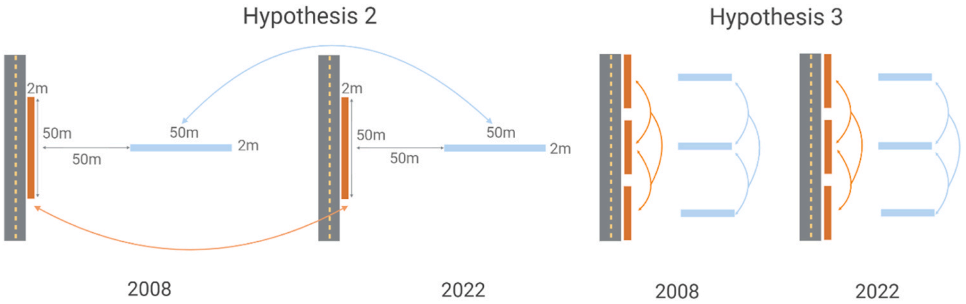

Fig. 1. Concept figure for the calculation of beta-diversity across time and space. To test hypothesis 2, the temporal change in community composition, we calculated beta-diversity using two identical plots between 2008 and 2022. This was done separately for disturbed and natural plots. In hypothesis 3, where we tested the temporal change in spatial community dissimilarity, beta-diversity was calculated among all possible plot pairs along the same elevation gradient and within the same habitat type (disturbed or natural) and the same year.
Created in BioRender.com.

2.3. *Statistical analysis*

All statistical analyses were performed in R version 4.3.2 (R Core Team, 2021).

Richness of native and non-native species, respectively, was calculated for each plot in each year. A generalized linear mixed-effects model including year, elevation (scaled between 0 and 1 across the three roads), plot type (disturbed or natural), species group (native or non-native), and all possible interactions as fixed effects, and the nested random effects of road, sample site, and plot identity was fit using the function "glmer" in the package "lmerTest" with a poisson family (Kuznetsova et al., 2017). To enable model convergence, the "bobyqa" optimizer was used and the maximum number of iterations was set to 1, 000,000. This correction was used for all subsequent generalized linear mixed-effects models. Two models were fit using the linear and the quadratic term of elevation (second-order polynomial of elevation), respectively, and then compared using a likelihood ratio test based on Chi-squared. For the better model, p-values for the fixed effects were calculated using likelihood ratio tests with the package "afex" (Singmann et al., 2023).

Assuming different responses of the two species status groups (native or non-native species), and to specifically test the first hypothesis referring to an increase of non-native (H1A), but not of native species (H1B) over time, separate generalized linear mixed-effects models for native and non-native species richness, respectively, were calculated, with the remaining fixed and random effects being identical to the model described before. By analyzing main effects as well as interactions between predictors, we could evaluate the individual parts of the hypothesis, specifically H1A. The same procedure was followed as above, and p-values for models with best fit for elevation were calculated.

To determine the effect of non-native species on the temporal change in community composition (H2), two different datasets were created from the vegetation surveys. One dataset included all species (native and non-native species together), while the other contained only native species. The package "betapart" (Baselga et al., 2021), specifically the "beta.pair.abund" function with Bray-Curtis dissimilarity, a robust abundance-based index (Schroeder and Jenkins, 2018), was used to calculate total beta-diversity between two identical plots in 2008 and 2022, as well as its two additive components of the abundance gradient and the balanced variation in abundance (Baselga, 2013). The balanced variation in abundance component refers to the substitution of a number of individuals of a species in one plot with the same number of another species in the compared plot. The abundance gradient component refers to the loss of individuals between plots. Balanced variation in abundance and the abundance gradient component are analogous to turnover and nestedness, respectively, in incidence-based analyses of beta-diversity (Baselga, 2013).

To test the second hypothesis, we fit three generalized linear mixed-effects models with a binomial family (Kuznetsova et al., 2017) to determine significant effects on total beta-diversity, the abundance gradient component, and the balanced variation in abundance component. The species group (whether it included all or only native species), plot type (disturbed or natural), elevation (scaled between 0 and 1 across the three roads), as well as all possible interactions were included as fixed effects. Again, interactions were included to assess the individual parts of the hypothesis separately. The road, sample site, and plot identity were included as nested random effects. Two models were again fit using the linear and the quadratic term of elevation, and then compared using a likelihood ratio test based on Chi-squared. P-values were calculated using type III likelihood ratio tests in the package "afex" (Singmann et al., 2023).

To test if non-native species spatially homogenize plant communities (H3), we calculated beta-diversity (total beta-diversity and its components as described above) for all plot pairs within the same elevation gradient and within the same plot type (disturbed or natural), separately for all species and for native species only (Fig. 1). Since we expected the homogenizing effect of non-native species to become stronger over time, we calculated beta-diversity for 2008 as well as for 2022 (hereafter called 'temporal change in spatial community dissimilarity'). For each metric of beta-diversity (total, abundance, and balance components), we fit a generalized linear mixed-effects model with a binomial family, species group (all vs native species), plot type (disturbed or natural), year, and all possible interactions as fixed effects, and nested road and the combination of plot identities as random effects. The same p-value calculation methods were used as described above.

3. Results

3.1. *Temporal changes in species occurrence and abundance*

In the 2008 survey, 151 native species (Disturbed plots: 127 species; Natural plots: 133 species) and 66 non-native species (Disturbed plots: 60 species; Natural plots: 44 species) were found. In the 2022 survey, 166 native species (Disturbed plots: 148 species; Natural plots: 138 species) and 67 non-native species (Disturbed plots: 63 species; Natural plots: 35 species) were found. The total number of native species found in at least one of the two surveys was 185 (Disturbed plots: 165 species; Natural plots: 164 species), the total number of non-native species was 85 (Disturbed plots: 79 species; Natural plots: 54 species).

Out of the 185 total native species, 110 species were perennials including trees, shrubs, and herbaceous species (most common: *Pinus canariensis, Forsskaolea angustifolia,* and *Pterocephalus lasiospermus*), and 75 species were annuals (most common: *Brachypodium distachyon, Erodium chium,* and *Lamarckia aurea*). For non-natives, 32 species were perennials (most common: *Hypochaeris glabra*, *Silene vulgaris*, and *Opuntia ficus-indica*) and 53 were annuals (most common: *Urospermum* *picroides, Sonchus oleraceus,* and *Erodium cicutarium*).

Mean abundance (number of individuals) per native species per plot in disturbed and natural plots decreased over time (Disturbed: 21.85 native individuals per species per plot in 2008 vs. 16.22 native individuals per species per plot in 2022; Natural: 31.86 vs. 14.97). Mean abundance per non-native species per plot in disturbed plots increased (13.43 non-native individuals per species per plot in 2008 vs. 16.79 non-native individuals per species per plot in 2022), while non-native species' mean abundance decreased in natural plots (17.05 vs. 11.58).

For native species found in both 2008 and 2022, there was an increase in occurrences per species (i.e. number of plots in which an individual species was found) in disturbed plots but no change in natural plots (Disturbed: +2.09 plots per species; Natural: −0.08 plots per species; for a list of native species occurrences by year, see Table A.1). This resulted in an increase of 230 total occurrences in disturbed plots and a decrease of 9 total occurrences in natural plots. Some of the most common native species found in both years include *Brachypodium distachyon*, *Pterocephalus lasiospermus*, *Pinus canariensis, Kleinia neriifolia*, *Forsskaolea angustifolia*, *Euphorbia lamarckii*, and *Bromus diandrus*.

Native species recorded only in 2022 occurred on average in more plots than those native species only observed in 2008 (Disturbed: +0.88 plots per species; Natural: +0.10 plots per species). This resulted in a higher total number of occurrences for species unique to 2022 compared to species solely observed in 2008 (Disturbed: +58 plots; Natural: +10 plots).

For non-native species found in both survey years, there was an average increase in occurrences per species in disturbed plots but a decrease in natural plots (Disturbed: +0.91 plots per species; Natural: −1.08 plots per species; for a list of non-native species occurrences by year, see Table A.2). This resulted in an increase of 40 total occurrences across disturbed plots, but a decrease of 27 total occurrences across natural plots. Some of the most common non-native species found in both years include *Urospermum picroides*, *Sonchus oleraceus*, *Erodium cicutarium*, *Hirschfeldia incana*, *Opuntia ficus-indica*, *Chenopodiastrum murale*, and *Lysimachia arvensis*.

Non-native species which were only observed in 2022 occurred on average in more plots in disturbed habitats, but in fewer plots in natural habitats compared to species found solely in 2008 (Disturbed: +0.26 plots per species; Natural: −0.89 plots per species). This resulted in a higher number of total occurrences for species unique to 2022 in disturbed habitats but fewer in natural habitats compared to species only observed in 2008 (Disturbed: +10; Natural: −26).

3.2. *Changes in species richness*

The model including all species (native and non-native species as distinct status groups) explained significantly more variation when including the quadratic term of elevation than the model including only the linear term (X^2=63.61, p <0.001). Due to the significant interactions between the species status group term (native or non-native) and plot

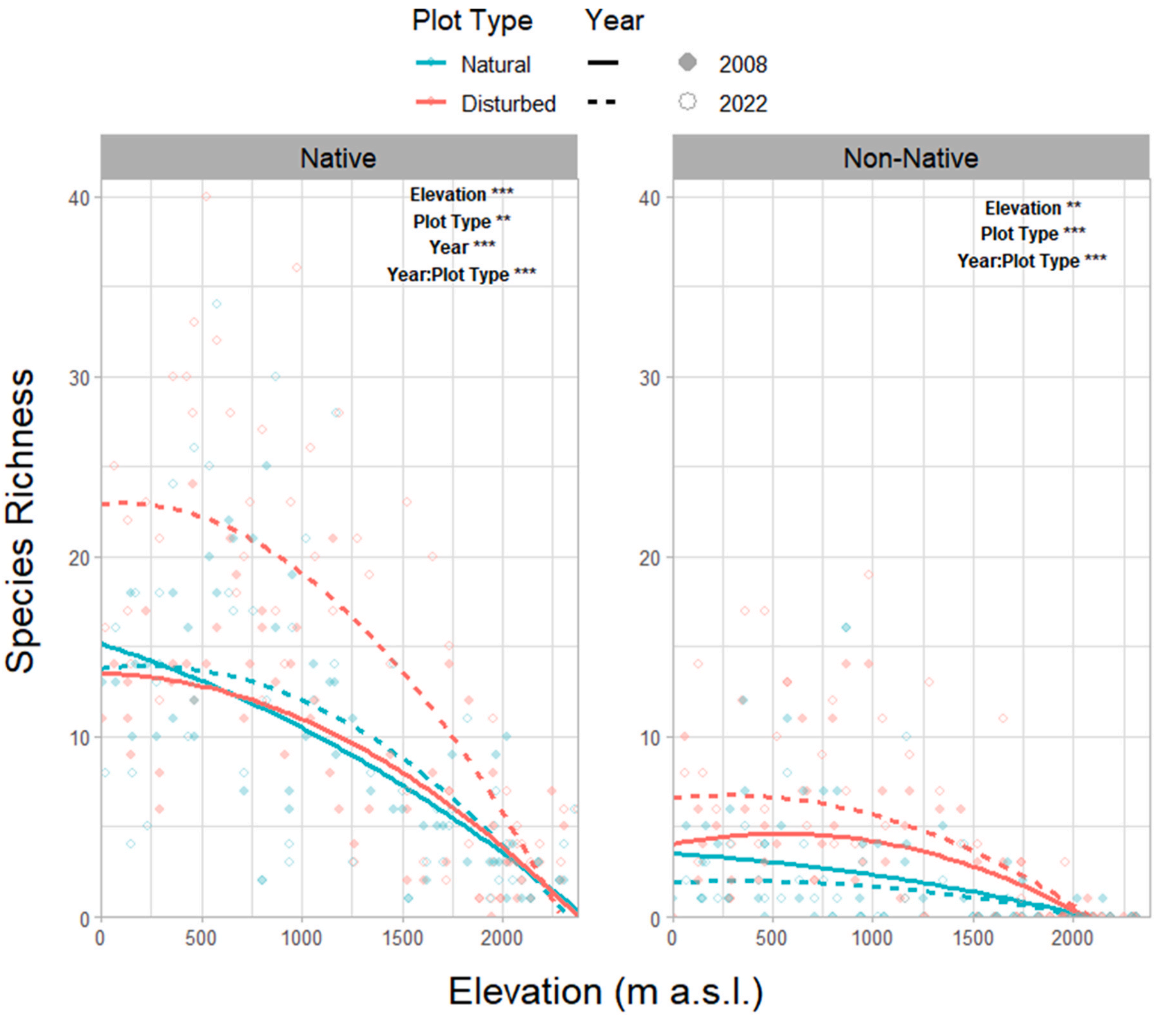

Fig. 2. Richness of (A) native and (B) non-native species by elevation, coded by plot type (disturbed or natural plots) and year. A quadratic adjustment for elevation provided a better fit for the models. Significant effects are listed inside each panel (* < 0.05, ** < 0.01, *** < 0.001). See Table A.3 for detailed statistical results. Symbols represent raw data, lines are based on model predictions.

type or elevation, respectively (Table A.3), separate models for native and non-native species were conducted in order to better determine the effect of these variables on species richness of each of the two groups. These models also explained more variation when including the quadratic elevation term (native species: X^2=19.93, p <0.001; non-native species: X^2=33.81, p <0.001; Table A.3).

In both years, native species richness declined as elevation increased, specifically in the upper part of the elevation gradient. In disturbed plots, native species richness was higher in 2022 compared to 2008, while there was no difference between native species richness in 2022 and 2008 in the natural plots (significant plot type-by-year interaction, Table A.3, Fig. 2A). Non-native species richness peaked in the lower half of the elevation gradient. It increased over time in disturbed plots, but decreased over time in natural plots. Overall, non-native species were more prevalent in disturbed plots than natural plots across both years (Fig. 2B).

3.3. Temporal change in community composition

The models for total temporal change in community composition, the abundance gradient component, and the balanced variation in abundance component did not explain significantly more variation using the quadratic term for elevation (total beta-diversity: X^2=1.38, p = 0.848, abundance gradient: X^2=2.10, p = 0.717, balanced variation in abundance: X^2=3.14, p = 0.534). Total temporal change in community composition increased with elevation in disturbed plots, but decreased with elevation in natural plots (significant elevation-by-plot type interaction, Table A.4, Fig. 3A). However, it was not affected by non-native species (no significant difference between all species together and native species only). Temporal change from the abundance gradient component increased steeply with elevation in disturbed plots and decreased slightly in natural plots (Fig. 3B). Temporal change from the balanced variation in abundance component did not vary significantly between plot types or with elevation (Fig. 3C). In disturbed plots, the balanced variation in abundance component contributed overall (i.e.

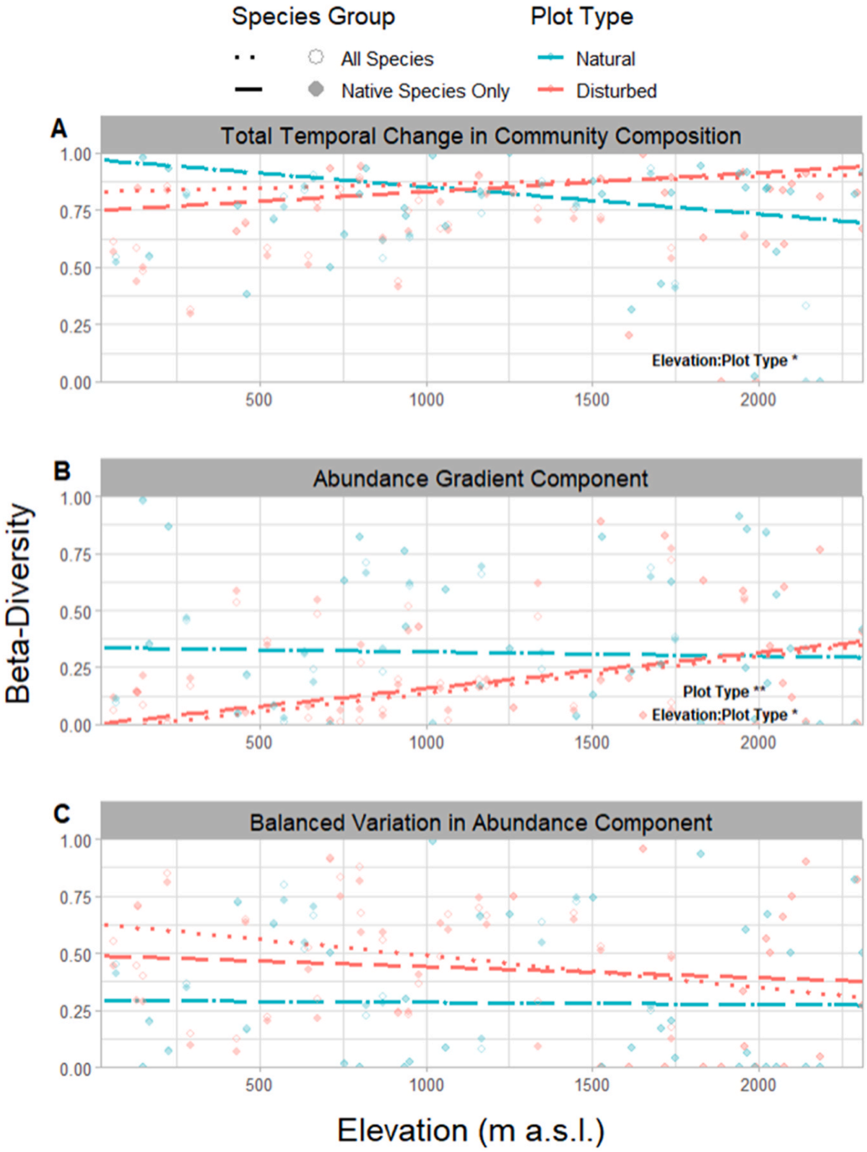

Fig. 3. Temporal change in community composition along the elevation gradient calculated as (A) total beta-diversity of identical plots between 2008 and 2022, and separately shown for each species group (all species together or native species only) and each plot type (natural or disturbed plots). Total beta-diversity was decomposed into the components of (B) the abundance gradient and (C) the balanced variation in abundance. Significant effects are listed inside each panel (* < 0.05, ** < 0.01, *** < 0.001). See Table A.4 for detailed statistical results. Symbols represent raw data, lines are based on model predictions. In natural plots, due to low numbers of non-native species, prediction lines for all species together and native species only are visually indistinguishable.

across the whole elevation gradient) approximately twice as much to total beta-diversity compared to the abundance gradient component, while in natural plots, the contribution of each component was essentially equivalent.

3.4. *Temporal change in spatial community dissimilarity*

Results of tests for temporal change in spatial community dissimilarity (i.e. dissimilarity values of all pairwise plot combinations within an elevation gradient, within the same plot type, and within the same year) indicate that non-native species did not significantly spatially homogenize plant communities in either of the two years, neither with regard to total dissimilarity (total beta-diversity) nor its two components (Table A.5). There was no difference in total spatial beta-diversity between years, but total beta-diversity was higher in natural plots than in disturbed plots across both years (Fig. 4A, Table A.5). For the two components of beta-diversity, we found significant, but opposing differences in spatial community dissimilarity between years. While the abundance gradient component was higher in 2022 than 2008, the balanced variation in abundance component was lower in 2022 than 2008 (Fig. 4B and C). This was mainly driven by differences in disturbed plots between years (significant year-by-plot type interaction for both components). The balanced variation in abundance component accounted for most of total beta-diversity in both natural and disturbed plots in both years.

4. Discussion

With our study, covering a 14-year time span, we aimed to describe changes in the elevational distribution patterns of non-native plant species and their influence on changes in community dissimilarity. Moreover, our unique study design allowed us to evaluate the influence of anthropogenic disturbance on these changes.

4.1. *Patterns of species richness*

Non-native species richness peaked at low to mid elevations and was higher in disturbed compared to natural habitats for both study years. These distribution patterns fall in line with previous studies from Tenerife (Arévalo et al., 2005; Bacaro et al., 2015; Haider et al., 2010) as well as from larger-scale studies across multiple mountain ranges (Seipel et al., 2012; Guo et al., 2018). Our results align with a plethora of observations that non-native species establishment is favored by environmental disturbance, which both reduces competition from native species and is in accord with the often-ruderal strategy of non-native species (Baker, 1974; Jauni et al., 2015; Lembrechts et al., 2016). We hypothesized that non-native species richness would increase over time, specifically towards mid-elevations and in disturbed habitats. While we observed an overall increase in non-native species over time in communities in disturbed habitats, we did not see this increase more pronounced at mid-elevations. Therefore, we can only partly confirm the first part of hypothesis 1 A (increase of non-native species richness), but none of the more specific expectations regarding the role of elevation and habitat.

In addition to non-native species, native species also increased over time in richness in disturbed habitats, in contrast to hypothesis 1B. This was not anticipated, as many previous studies suggest that native species are negatively impacted by anthropogenic disturbance (Chiuffo et al., 2018; Geppert et al., 2021; Everingham et al., 2019; Jauni et al., 2015). However, other studies demonstrated that some levels of disturbance may also enhance native species richness, invoking the intermediate disturbance hypothesis (Araujo Calçada et al., 2015; Escobedo et al., 2021; Pellegrini et al., 2021; Yuan et al., 2016). This might apply more specifically to annual species, which are the most typical life form among ruderal species, and which increased in number the most in our study (Fig. A.1). Additionally, this result is in line with a previous study suggesting that the Canary Islands see strong recolonization of disturbed habitats by native species (Fernández-Palacios et al., 2023).

The total number of non-native species in the two study years did not differ substantially, but in disturbed habitats along roadsides, the number of occupied plots per non-native species increased (Table A.2). This suggests that, along roadsides, non-native species were spreading within their elevational niche since the first study year and that they seem to build stable populations, a finding corroborated by other studies (Iseli et al., 2023; Merow et al., 2017). This also aligns closely with studies indicating that roadways can often facilitate the spread of non-native species through vehicle traffic and human-mediated seed dispersal (Lemke et al., 2019, Mortensen, et al., 2009). However, native species also increased in the number of occupied plots in disturbed habitats, suggesting that these methods of propagule transportation benefit both native and non-native species (Lembrechts et al., 2017).

For communities in natural habitats, we predicted that non-native species richness would also increase over time, most pronounced at mid-elevations, but in a more diminished pattern compared to disturbed habitats. Our results showed the opposite, with communities in natural habitats containing fewer non-native species in the second study year.

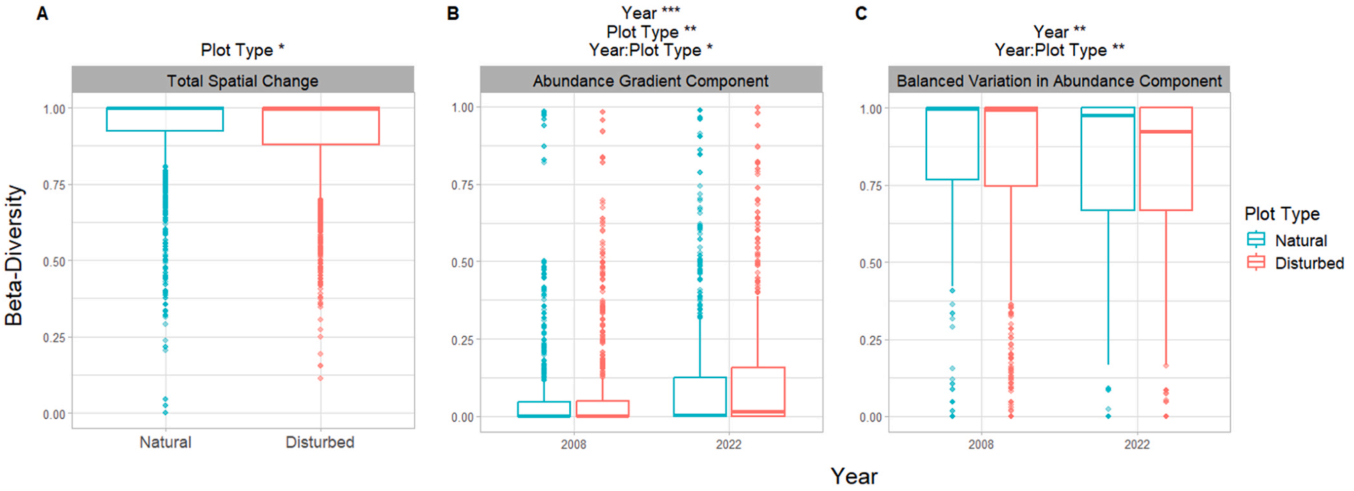

Fig. 4. Temporal change in spatial community dissimilarity within elevation gradients between 2008 and 2022 by (A) total beta-diversity, (B) the abundance gradient component, and (C) the balanced variation in abundance component. Significant effects are listed above each panel (* < 0.05, ** < 0.01, *** < 0.001). See Table A.5 for detailed statistical results.

There are a few possibilities as to why non-native species declined in natural sites over the time of this study. Environmental conditions may play a role in the decline of non-native species in natural habitats, especially in the warm, arid conditions of the south face of Tenerife (Liu et al., 2017; Valliere et al., 2019). Dry conditions prevailed for several seasons between 2008 and 2022 (total precipitation between 2005 and 2007: 717.2 mm, total precipitation between 2019 and 2021: 202.2 mm, Lawrimore et al., 2011), likely causing non-native plants to disappear, specifically annual species (Fig. A.2). Both the lower mean abundance of non-native species within the communities (Table A.2) and the lower number of plots occupied by non-native species in the later study year (Table A.2) are likely to reflect these challenging environmental conditions. Additionally, it might take time for non-native species to re-establish in natural habitats, since they typically invade from disturbed into natural habitats, with horizontal propagule transportation from roadside into adjacent natural environments typically occurring less frequently than vertical transportation along roadsides (McDougall et al., 2018). While native species are well-established in natural sites and were able to maintain species richness for both perennials and annuals (Fig. A.1), they seem to also be affected by these conditions due to the stark reduction in the native species' local abundance. However, this did not result in a net loss of native species in the natural communities over time or a change in occurrences per species. Native species have been shown to be more tolerant to natural stressors compared to non-native species (Chiuffo et al., 2018), suggesting that native species in these communities may have been more resistant to periods of dry conditions than non-native species.

Interestingly, the above-mentioned stressful environmental conditions did not result in a decrease in species richness in disturbed habitats, neither for native nor non-native species. While it is unlikely that climate has no effect on disturbed habitats, the enhanced propagule pressure likely compensates for the negative effects of prevailing dry conditions.

4.2. Temporal change in community composition

Although non-native species richness in disturbed habitats increased significantly between 2008 and 2022, there was no signal of non-native species influencing the extent of temporal change in community composition. This suggests that the observed changes along roadsides mainly result from the increase in native species, their turnover between years, as well as from changes in their abundances. In disturbed habitats, the temporal change in community composition was predominantly caused by the balanced variation in abundance, pointing towards a pronounced species turnover (Kaarlejärvi et al., 2021). Indeed, 55 native species (33 % of all native species) occurred in only one of the two study years. Although the relative importance of the balanced variation in abundance component for total temporal change in community composition was larger for annual species compared to perennials (Figs. A.3 and A.4), the higher number of perennials in our dataset determined the overall change. In contrast, abundance gradients, i.e. losses or gains in individual species' abundances, were overall of minor importance in disturbed habitats. Still, community change resulting from shifts in individual species' abundances (abundance gradient component) surprisingly increased at higher elevations. High-elevation communities were predominantly composed of native species, for which we found an overall decrease in mean abundance per plot between years. This elevational pattern holds for perennial species (the major life form of native species and typical for high elevations), but not for annuals (Fig. A.3 and A.4). The decrease in native species' abundances is likely to be caused by the extraordinary dry conditions described before. While propagule dispersal along roadsides might support the short-term establishment of annual species at lower elevations, even with increasing local species richness, reduced dispersal at high elevations cannot compensate for the loss of individuals through stressful periods.

In natural habitats, temporal change in community composition exhibited more even contributions from shifts in species' abundances and species turnover. Total temporal change in community composition decreased with elevation in natural habitats, resulting from the elevational decrease of the abundance gradient component, while species turnover was constant and lower across all elevations. While the strong decline of mean species abundance per plot in the later study year explains the higher importance of the abundance gradient component in natural compared to disturbed habitats, the elevational pattern is likely to be related to species life forms, with perennials paralleling the elevational cline, but not annuals.

Overall, the temporal change in community composition was high across the entire elevation gradient, but the lack of significant impact of non-native species makes it clear that shifts in the native community were the driving force for these changes. Therefore, we must completely reject our second hypothesis, expecting that community changes over time were driven by the group of non-native species. This was an unexpected outcome and demonstrates that native species are also heavily influenced by varying environmental conditions (Chiuffo et al., 2018; Jauni et al., 2015).

4.3. Temporal changes in spatial community dissimilarity

We hypothesized that increasing non-native species richness from 2008 to 2022 would lead, in the later year, to a reduction of the dissimilarity between communities within each of the three elevation gradients, and would therefore spatially homogenize the plant communities (H3). However, all components of temporal change in spatial community dissimilarity did not display any significant effects of non-native species or lead to clear signals of community homogenization. We therefore reject hypothesis 3, which is especially surprising for disturbed habitats where, not only did the number of non-native species increase over time, but also their occurrences per species. Other studies that focused on islands have resulted in a mix of both biotic homogenization and differentiation (Castro and Jaksic, 2008; Otto et al., 2020), though one additionally found non-significant results (Otto et al., 2020). Overall, our result of insignificant effects of non-native species is contrary to the majority of studies that find homogenization of communities as a result of non-native species introduction (Kortz and Magurran, 2019; Kramer et al., 2023; Pauchard et al., 2013; Qian and Qian, 2022; Stotz et al., 2019), and to the minority of studies that find differentiation of communities (Blowes et al., 2024; McKinney, 2004).

Despite the lack of non-native species' influence, we observed significant temporal changes. Differences in individual species' abundances between the communities within an elevation gradient (abundance gradient component) were higher in 2022 than 2008, but species turnover between communities (balanced variation in abundance component) was lower in the later year. Although species richness was higher in 2022, it is likely that the increase in the contribution of the abundance gradient component is due to an overall decrease in the abundance of both native and non-native species over time.

For disturbed habitats, the lower turnover of species across the elevation gradients in 2022 suggests that while native and non-native species richness in the communities increased, more of the same species were found in more communities along the elevation gradients (Freeman et al., 2018; Lenoir et al., 2008). Transportation and anthropogenic disturbance via roadways thus benefit both native and non-native species (Dainese et al., 2017; Everingham et al., 2019; Lembrechts et al., 2017), allowing both species groups to fill additional niches along elevation gradients. In contrast, in natural habitats, species turnover was also lower in 2022, but native species richness in the communities did not significantly change. This suggests that in natural habitats, community dissimilarity is not only caused by some native species spreading along the elevation gradient and occupying more communities, but also by some more rare species disappearing. Overall, species turnover contributed substantially more to total temporal change in spatial community dissimilarity which is unsurprising due to high species diversity and heterogeneity along the elevation gradients.

Independent of the sampling year, communities in natural habitats were more dissimilar to each other than communities in disturbed habitats which is likely due to the homogeneity of roadsides as compared to natural habitats (Delgado et al., 2007; Müllerová et al., 2011).

4.4. Conclusions

Despite a significant increase in non-native species richness in disturbed habitats between 2008 and 2022, their impacts on community composition over time were not elucidated. It is apparent through this increase in non-native species richness that there are changes occurring in these plant communities, but the dynamic nature of the native community, representing the majority of species present, as well as the relatively short time span, clouds our ability to detect both temporal and spatial change in community composition. Although islands have been shown to harbor a disproportionally high number of non-native species (Lonsdale, 1999), it is clear that their effects on resident communities are not necessarily tied directly to species richness. Climate change will likely make these relationships challenging to decipher as it causes disruptions in both the native and non-native communities (Diez et al., 2012; Dullinger et al., 2012; Freeman et al., 2018; Lenoir et al., 2008).

While this study was only conducted between two time points, we found that the patterns of temporal change in community composition are reflected in responses of perennial species, those which are more likely to be present across long time scales (Fig. A.3). However, the stochastic nature of both native and non-native annual species (Fig. A.4) as well as periods of climate abnormalities are important considerations when evaluating the permanence of changes in community composition over time.

Anthropogenic disturbance in the form of roadways undoubtedly plays an important role in the movement of both native and non-native species along elevation gradients (Lembrechts et al., 2017; Lemke, et al., 2019; Mortensen et al., 2009). We expect that species will continue to shift elevationally, though detecting resulting changes in community composition will likely continue to be challenging with the impacts of multiple global change drivers as well as the stochasticity of their interactions. These drivers, specifically anthropogenic disturbance, are not unique to our study site and we expect that this also perpetuates shifts in communities in other mountain regions. More systematic and temporal studies, especially those such as this which include not only presence-absences but also species abundances, are necessary to untangle the interaction of non-native species spread and global change drivers as they shift community composition.

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CRediT authorship contribution statement

Amanda Ratier Backes: Investigation, Writing – review & editing. **Sylvia Haider:** Conceptualization, Funding acquisition, Investigation, Methodology, Supervision, Writing – review & editing. **José Ramón Arévalo:** Investigation, Methodology, Writing – review & editing. **Meike Buhaly:** Conceptualization, Formal analysis, Investigation, Visualization, Writing – original draft, Writing – review & editing.

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.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.ppees.2024.125845.

Data availability

The data is available on Zenodo (zenodo.org/doi/10.5281/zenodo.5529071)

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