



# Human impact, climate and dispersal strategies determine plant invasion on islands

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## Abstract

**Aim:** Biological invasions are likely determined by species dispersal strategies as well as environmental characteristics of a recipient region, especially climate and human impact. However, the contribution of climatic factors, human impact, and dispersal strategies in driving invasion processes is still controversial and not well embedded in the existing theoretical considerations. Here, we study how climate, species dispersal strategies, and human impact determine plant invasion processes on islands distributed in all major oceans in the context of directional ecological filtering.

**Location:** Six mountainous, tropical, and subtropical islands in three major oceans: Island of Hawai'i and Maui (Pacific), Tenerife and La Palma (Atlantic), and La Réunion and Socotra (Indian Ocean).

**Taxon:** Vascular Plants.

**Methods:** We recorded 360 non-native species in 218 plots along roadside elevational transects covering the major temperature, precipitation and human impact (i.e., road density) gradients of the islands. We collected dispersal strategies for a majority of the recorded species and calculated the environmental niche per species using a hypervolume approach.

**Results:** Non-native species' generalism (i.e., mean community niche width) increased with precipitation, elevation and human impact but showed no relationship with temperature. Increasing precipitation led to environmental filtering of non-native species resulting in more generalist species under high precipitation conditions. We found no directional filtering for temperature but an optimum range of most species between 10 and 20°C. Niche widths of non-native species increased with the prevalence of certain dispersal strategies, particularly anemochory and anthropochory.

Severin D. H. Irl and Andreas H. Schweiger are equal contributions.

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**Main conclusions:** Plant invasion on tropical and subtropical islands seems to be mainly driven by precipitation and human impact, while temperature seems to be of little importance. Furthermore, anemochory and anthropochory are dispersal strategies associated with large niche widths of non-native species. Our study allows a more detailed look at the mechanisms behind directional ecological filtering of non-native plant species in non-temperature-limited ecosystems.

#### KEYWORDS

biogeography, climate, dispersal, invasion ecology, island, niche, plant functional traits, roads

## 1 | INTRODUCTION

The erosion of biogeographic barriers by human activities is a defining element of the Anthropocene that has led to an unprecedented exchange of species across oceans and continents (van Kleunen et al., 2015; Kueffer, 2017; Lewis & Maslin, 2015). Abiotic, especially climatic, characteristics of the recipient region strongly control the establishment and spread of non-native plant species (Alexander et al., 2011; Petitpierre et al., 2012; Zefferman et al., 2015) besides propagule pressure and biotic characteristics (Catford et al., 2009) as well as anthropogenic activities (Blackburn et al., 2016; Moser et al., 2018). However, our general understanding of the interplay between climatic influences and human activities on plant invasion between as well as within recipient regions is insufficient so far, although theoretical considerations like the concept of *directional ecological filtering* (Alexander et al., 2011), the generalization of invasions along steep environmental gradients as *invasion syndromes* (Kueffer et al., 2013) and the notion of natural and anthropogenic disturbance regimes acting as catalysts of invasion dynamics (Jentsch & White, 2019) provide important conceptual cornerstones regarding abiotic filtering of non-native species along environmental gradients. Furthermore, the relative contribution of climatic factors versus dispersal strategies in driving plant invasion processes is still controversial and equivocally embedded in the existing theoretical considerations so far.

The theoretical concept of *directional ecological filtering* stresses the importance of abiotic conditions in filtering non-native species along environmental gradients (Alexander et al., 2011). The authors demonstrate that with increasing elevation (i.e., increasing geographic and ecological distance from the lowland introduction source) non-native species with a wide environmental amplitude (i.e., generalists) become more and more important in the non-native species pool because non-native specialists (i.e., species with a narrow environmental amplitude) are selectively filtered out along the environmental gradient. As a consequence, under unfavorable conditions at high elevations, non-native high elevation specialists are underrepresented in comparison to non-native generalists. Our study sets out to disentangle the different layers included in

directional ecological filtering: (a) the indirect but integrative effect of elevation *per se* and (b) direct environmental effects, e.g., driven by climate and the intensity of human impact, that change along an elevational gradient, often in a non-linear way.

The process of species sorting along elevational gradients described by directional ecological filtering has been an important contribution to plant invasion biology. Nevertheless, the integrative nature of elevation reflects a wide series of independent and partly non-linear trajectories and thresholds in multiple abiotic conditions, e.g., temperature, frost, wind speed, precipitation, UV radiation, cloudiness, atmospheric pressure, etc. (Körner, 2007). This complicates identifying the actual abiotic determinants of ecological filtering. Therefore, for a better mechanistic understanding of the processes behind directional ecological filtering, it is paramount to disentangle elevation from biotic and abiotic drivers behind species sorting (Jakobs et al., 2010; Lembrechts et al., 2017; Seipel et al., 2015). We choose high elevation islands as model systems because of their isolated and replicative character (MacArthur & Wilson, 1967), their recognized position as hotspots of global plant invasion (Dawson et al., 2017) and their often steep and non-linear climatic and disturbance gradients within the recipient regions on small spatial scale driven by differences in trade wind exposure (Irl et al., 2015; Weigel et al., 2018) and human activity. This allows us to separate the influence of different abiotic drivers (i.e., temperature and precipitation), human impact, and species dispersal strategies (Seipel et al., 2015; Steinbauer et al., 2017). Particularly, the environmental and climatic diversity found on high elevation islands characterize these systems as condensed continents, referred to as *mini-continents* (Irl et al., 2015) as well as a wide range and non-random distribution of human influences and activities (Caujapé-Castells et al., 2010).

How human activities on the scale of plant communities affect and alter the spread and establishment of non-native species within a recipient region (e.g., an island) is still under scrutiny. This is because geographic entities (e.g., islands or countries) are often taken as a reference by invasion biologists for large-scale assessments (e.g. Blackburn et al., 2016; Kueffer et al., 2010; Moser et al., 2018). Independent of scale, areas of high human densities will increase the likelihood of non-native species to establish (Spear et al.,

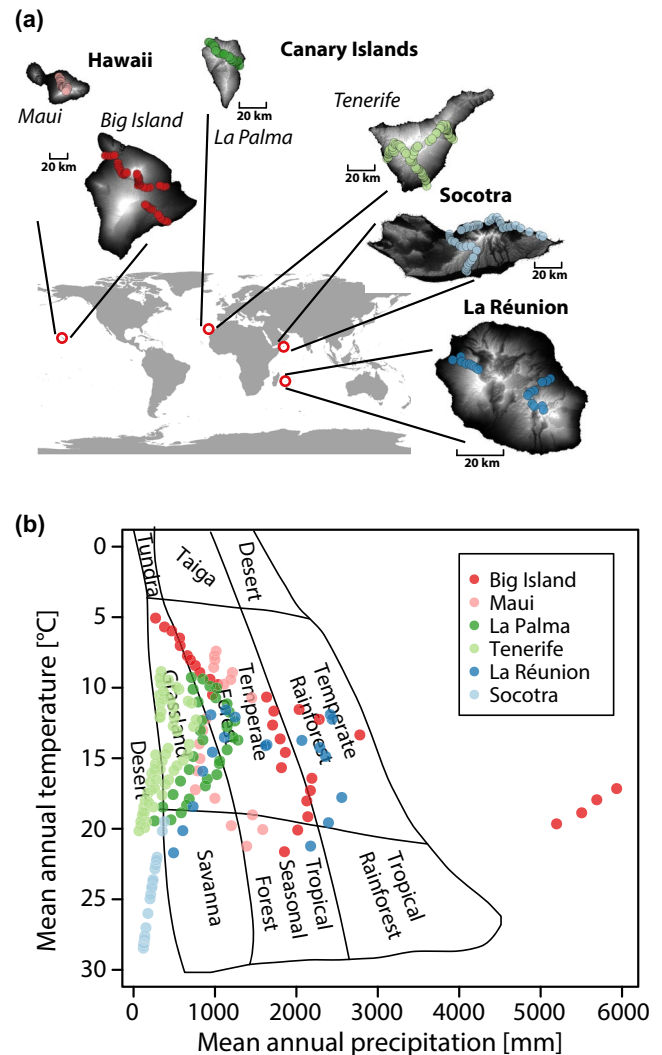
2013). More specifically, non-native specialists establish and persist in areas of high human densities because such areas are generally the core areas of introduction and establishment for a wide range of non-natives (Pauchard et al., 2009). We assume that non-native generalists will, as a result of their environmental tolerance and possibly also better dispersal strategies (Moravcová et al., 2015), be able to spread to areas that have a lower human footprint, leading to larger niche widths of non-natives in natural and undisturbed areas. Indeed, it is likely that both abiotic as well as anthropogenic influences act simultaneously on processes shaping biological invasions in plant communities. Deciphering their individual contributions will help our mechanistic understanding of biological invasions.

We argue that by using roadsides on oceanic islands across various archipelagos, we have standardized, repeatable settings that reduce the blurring effect of biotic interactions on the abiotic signal (Lembrechts et al., 2017; Poll et al., 2009). This allows identifying the potential climatic conditions that non-native species could spread into before they invade natural areas where biotic interactions such as competition (Haider et al., 2018; McDougall et al., 2018) but also plant associated mutualisms such as mycorrhizal fungi (Clavel et al., 2020) become more relevant. In this study, we use the aforementioned characteristics of islands as model systems (Burns, 2015) and roads across elevational gradients as experimental entities to study the drivers and dynamics of invasion processes to address the following research questions: (a) Which abiotic variables drive increasing generalism of non-native plant species described by the directional ecological filtering concept within and between oceanic islands? (b) Do anthropogenic drivers alter the pattern identified by directional ecological filtering within and between oceanic islands? (c) Does the prevalence of certain dispersal strategies lead to increasing generalism in non-native plant species?

## 2 | MATERIALS AND METHODS

### 2.1 | Study areas

In a coordinated effort, we studied 13 elevational roadside transects on 6 subtropical and tropical islands in 4 archipelagos across 3 oceans and major bioclimatic regions (Figure 1, Table 1, 218 vegetation records covering 360 non-natives species of 762 species). All roads that were sampled were two-lane paved mountain roads. Three of the four sampled archipelagos are of volcanic origin (Hawai'i, Canary Islands and La Réunion). Socotra is a continental fragment. All islands are high elevation islands covering a wide range of climatic conditions (Irl, 2014). Across all studied islands, mean annual temperature (MAT) ranges from around 5 to around 28°C and mean annual precipitation (MAP) from around 100 to almost 6000 mm, respectively (Table 1). All islands are affected by an asymmetric distribution of precipitation along the elevational gradient, depending on the orientation to trade winds, i.e., Canary Islands, Hawai'i and La Réunion, or monsoonal winds (Socotra). This asymmetry facilitates disentangling the key environmental drivers changing along



**FIGURE 1** (a) Map of study regions represented by six islands from four archipelagos, including plot locations. (b) Although located on islands, our plots span climatic space of global magnitude, as illustrated by the Whittaker plot (Weigelt et al., 2013). The four outlier points on the mean annual precipitation axis are located in the hyper-humid zone of trade wind clouds on the windward side of Hawai'i Island, Hawai'i. Note the differing scale bars per island. All maps drawn using the WGS 84 projection.

elevation. Humans populate all islands. As a result, all islands have a relatively large but varying network of roads.

### 2.2 | Sampling design

Biotic interactions in natural communities can strongly blur the effects of climate forcing on the establishment and spread of non-native plant species (Catford et al., 2009). For this reason, we focus on roadside communities, where frequent disturbances strongly diminish the effects of biotic interactions (Lembrechts et al., 2017; Poll et al., 2009). To standardize for local disturbances, we sampled elevational transects in roadside plots (Bacaro et al., 2015; Jakobs et al., 2010; Maděra et al., 2013) because they provide not only repeatable

**TABLE 1** List of all sampled islands and the number of non-native species, all species collected, and % non-native species on each respective island. Additionally, we provide selected environmental features of all transects within each island (minimum and maximum mean annual temperature, mean annual precipitation and elevation)

Archipelago (Ocean)	Island	Transects per island	Non-native species collected	All species collected	% Non-natives	Min.-Max. mean annual temperature (°C)	Min.-Max. mean annual precipitation (mm)	Min.-Max. elevation (m a.s.l.)	Island area (km <sup>2</sup> )	Island age (My)
Canary Islands (Atlantic)	Tenerife	3	61	232	26	8.8–20.1	96–799	5–2250	2034	11.5
Canary Islands (Atlantic)	La Palma	2	40	244	16	9.2–19.4	287–1312	161–2281	706	1.7
Hawai'i (Pacific)	Maui	1	88	102	86	7.3–21.1	789–1617	364–2958	1883	1.5
Hawai'i (Pacific)	Big Island	3	146	168	87	4.9–23.7	272–5964	21–3747	10430	0.6
Socotra (Indian Ocean)	Socotra	2	7	135	5	19.4–28.3	150–410	3–986	3625	Continental fragment
Mascarenes (Indian Ocean)	La Réunion	2	140	229	61	11.5–21.6	522–2588	382–2366	2512	3

settings ideal for comparing non-native species establishment even across biogeographic regions (Alexander et al., 2011; Seipel et al., 2012) but also provide habitat for endemic plant species such as roadside cliffs that shelter endemics from anthropogenic disturbances and introduced herbivores (Irl et al., 2014). Roads are often regarded as important vectors for the spread of non-native species (Walentowitz et al., 2019). In this context, human impact, which is measured as road density per km<sup>2</sup>, represents the probability of introduction of non-native species to a certain location of an island. Figuratively speaking, where human impact is high, the 'introduction gateway' is farther open for a given non-native species.

We used standardized roadside plots to ensure comparability between study areas. We collected data from previously published data for Hawai'i from Jakobs et al. (2010), for Tenerife from Bacaro et al., (2015), and for Socotra from Maděra et al., (2013). Data that were collected exclusively for this study and previously unpublished can be found in Table S2a. On Hawaii, the Canary Islands and La Réunion roadsides were sampled using plots of 2 × 50 m (=100 m<sup>2</sup>) with the longer side being placed parallel to the road. A different plot shape (20 × 5 m = 100 m<sup>2</sup>) was chosen on Socotra with the longer side placed along the road (see Maděra et al., 2013 for details). We recorded all plant species within each plot. Data collection took place in 2007 (Tenerife, Hawai'i), 2011 (Socotra), 2012 (Maui), 2013 (La Palma), and 2015 (La Réunion). The sampling design resulted in 218 roadside plots with 16.8 ± 7.0 roadside plots per elevational transect. Species nomenclature was harmonized using Kew's Plant List (The Plant List, 2015). We determined the status as non-native using Acebes Ginovés et al., (2010) for the Canary Islands, Wagner et al., (2005) for Hawai'i, Boulet (2015) for La Réunion, and Miller and Morris (2004) and Senan et al., (2012) for Socotra.

Transects covered substantial elevational and climate gradients of continental magnitude (Figure 1, Table 1), highlighting the representability of this study. Overlap in non-native species composition was generally quite low between archipelagos (Table S2b). We recorded 360 non-native species (47% of all recorded species) in 218 plots. We found most non-native species to be restricted to one archipelago (314 species, 87.2%), while only few occurred on two (42 species, 11.7%) or three archipelagos (2 species, <1%). The two most widespread species were *Bidens pilosa* and *Rumex acetosella* occurring on Hawai'i, La Réunion, and the Canary Islands—both considered global invasive species in mountainous areas (Seipel et al., 2012). Six species had >30 occurrence records (*Hypochaeris radicata*: 40 [18% of plots], *Plantago lanceolata*: 38 [17% of plots], *Pennisetum clandestinum*: 35 [16% of plots], *Holcus lanatus*: 32 [15% of plots], *Senecio madagascariensis*: 32 [15% of plots], *Sonchus oleraceus*: 31 [14% of plots]). For a list of all species' occurrence records see Table S2b.

### 2.3 | Dispersal strategies

We obtained information on dispersal strategies (anemochory, zoochory, hydrochory, and anthropochory) for 191 of the 360 non-native plant species in our data set (53%). Anthropochory here



defines species dispersal by humans that can be either accidental when seeds easily attach to clothing, footwear, tires, vehicles or through agricultural practices or intentional species spread through planting for ornamental and agricultural purposes (Faliński, 1972). Data for most species were extracted from CABI invasive species compendium ([www.cabi.org/isc](http://www.cabi.org/isc)), a comprehensive, global database on biological and ecological characteristics of invasive species. A list of all dispersal strategies per species can be found in Table S3. When no information was available from this data base, we conducted web searches (these additional web sources are listed in Table S3). If necessary, multiple dispersal categories were assigned per species because many species have more than one dispersal strategy.

## 2.4 | Environmental data

Climate data, i.e., MAT and MAP, for the Canary Islands were taken from interpolated meteorological stations presented in Irl et al., (2015) with a resolution of  $100 \times 100$  m. For Hawai'i, we downloaded the corresponding GIS layers and extracted the point values for each georeferenced plot with a resolution of  $250 \times 250$  m (Giambelluca et al., 2013, 2014). The climate data for La Réunion were provided by Météo France (French National Institute for Meteorology and Climatology) and for Socotra by Scholte and de Geest (2010) and unpublished data with a resolution of  $900 \times 900$  m. Per plot climatic data can be accessed in Table S2c.

We approximated human impact as road density (Foxcroft et al., 2011) by measuring per  $1 \text{ km}^2$  raster cell the length of all roads. The more roads are located in a raster cell, the higher the road density value, and thus the higher the human impact (Basille et al., 2013). Here, high road density and thus human impact is associated with a high probability of introduction of non-native species (Guido et al., 2016; Pauchard et al., 2009). We assigned a road density value to each plot by using its location per raster cell to extract the road density value in a GIS framework. Other factors of human impact such as human population size or socioeconomic variables that have been shown to be important for invasion processes on the island scale (e.g., Kueffer et al., 2010 or Blackburn et al., 2016) are too coarse to be applied on the plot scale we are working on and, thus, were not considered for the analyses.

## 2.5 | Estimation of niche width

Climatic niche width of the particular species was estimated by following Hutchinson's concept where species niche is defined as an  $n$ -dimensional space (hypervolume) in which a species is able to exist under consideration of biotic interactions (Hutchinson, 1957). Following this concept, we quantified niche space for each species by using the hypervolume approach of Blonder and Harris (2019) based on MAP and MAT as input variables. Hypervolumes were calculated for each species with more than three records based on a box kernel density estimation using the *hypervolume()* command

of the *hypervolume* R package (4.0.3, Blonder & Harris, 2019). The Silverman bandwidth estimator was used to estimate the bandwidths for the box kernel density estimation of each species. This estimator is defined as  $1.06 \cdot \text{sd}(X) \cdot m^{-1/5}$  with  $m$  being the number of observations and  $X$  is the data vector in each input variable. Both input variables, MAP and MAT, were standardized for hypervolume estimation to ensure that hypervolume dimensions are comparable. Elevational range of each species was calculated by subtracting the lowest elevational occurrences per species from the highest. Mean community niche width of the investigated non-native plant communities was subsequently calculated as the mean of the individual hypervolumes or elevational ranges of all species per plot.

We calculated temperature and precipitation range realized by each species across the six investigated islands as well as the global temperature and precipitation range realized by the investigated species. Species' global temperature and precipitation ranges were estimated by combining species distribution information obtained from the Botanical Information and Ecology Network (BIEN) database (via the *BIEN* R package, 1.2.4, see Figure S7; Maitner, 2020) with climatic information on MAT and MAP obtained from the Worldclim (bioclim) dataset with a 2.5 min resolution (Fick & Hijmans, 2017).

## 2.6 | Statistical analysis

We used simple and multiple linear regression models to assess the effect of climate, human influence and dispersal strategy on species richness and mean community niche width of non-native plants. Predictor variables were not transformed unless the model plots and diagnostics indicated the need of predictor transformation. For this we tested quadratic ( $x^2$  and  $x^2+x$ ) as well as log-transformed data against untransformed data.

We applied linear mixed-effect models by using geographic sampling location (expressed by transect ID) as random effect (random slope and intercept). With this we account for island-specific differences in how climate, human impact and dispersal strategies influence invasion processes. We quantified the proportion of explained variation for the linear mixed-effect models by calculating Pseudo- $R^2$  for generalized mixed-effect models using the *r.squaredGLMM()* function from the *MuMIn*-R-package (1.43.17; Barton, 2020). The proportion of explained variation is thereby deconstructed into a Marginal  $R^2$  that is the contribution of variance that is explained by the fixed effect alone (e.g., MAT or MAP) and a Conditional  $R^2$  that quantifies the variance explained by the fixed effect plus the random effect.

We used variance partitioning to decipher the contribution of dispersal strategies versus climate drivers versus human impact in explaining mean community niche width of non-native species. We therefore selected the best predictors based on Marginal  $R^2$  and AIC from the linear mixed-effect models and aggregated these variables to the three grouped predictor variables dispersal strategies, climate and human impact. Variation partitioning was performed using the *varpart()* function included in the *vegan* R-package (2.56; Oksanen



et al., 2019). The proportional Venn diagram was drawn with *eulerAPE* (Micallef & Rodgers, 2014).

We used non-parametric ANOVA (Kruskal–Wallis Test) to test differences in species' climatic niche (hypervolume) and elevational range between the different dispersal strategies. We used generalized linear models with a binomial distribution to test the effects of species-specific niche width (i.e., hypervolume) on the probability of being dispersed by wind, water, animals, and humans, respectively.

All analyses and statistical tests were performed in the R environment (4.0.2; R Core Team, 2020) with a level of significance of  $\alpha = 0.05$ .

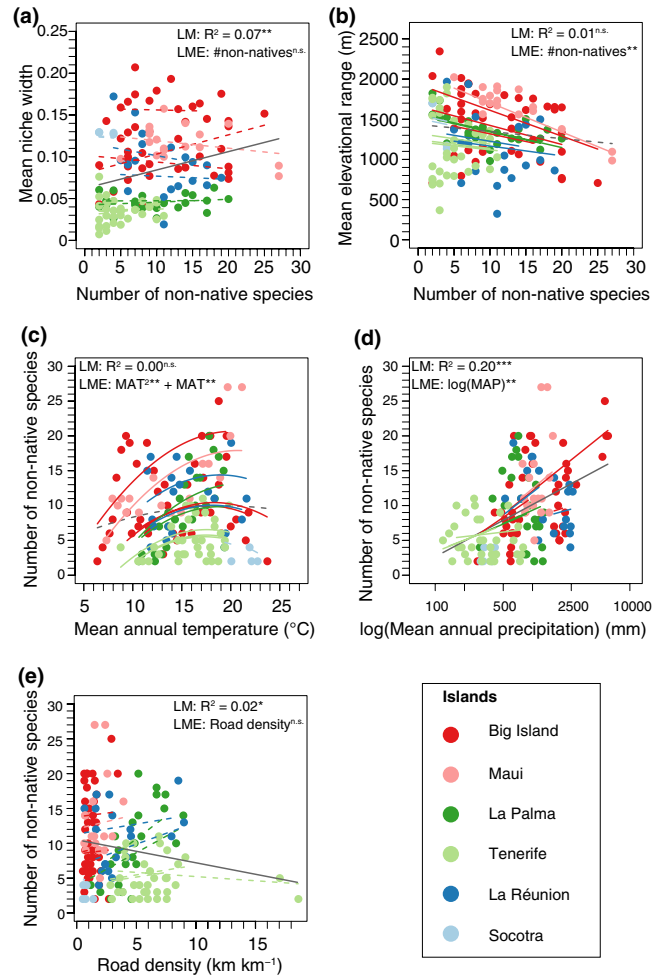
### 3 | RESULTS

#### 3.1 | The effects of climate and human impact on non-native species richness and niche width

Non-native species richness showed a positive effect on non-native community niche width (Adjusted  $R^2 = 0.07$ ,  $p = 0.001$ ) but showed no effect on the community mean elevational range (Adjusted  $R^2 = 0.01$ ,  $p = 0.12$ ) when pooling all data from all islands. The positive effect of non-native species richness on non-native community niche width disappeared while its effect on mean elevational range was significant for the partially pooled data, i.e., when accounting for transect and island identity in a linear mixed-effect model (Marginal  $R^2 = 4.96 \times 10^{-5}$ ,  $p = 0.93$  and marginal  $R = 0.08$ ,  $p = .0015$ , respectively, Figure 2a,b). Non-native species richness furthermore had a hump-shaped correlation with MAT for the partially pooled data but no significant relationship was detected for the pooled data (marginal  $R^2 = 0.13$ ,  $p < 0.01$  for the partially pooled data and adjusted  $R^2 = 0.002$ ,  $p > 0.3$  for the pooled data, Figure 2c, Table 2 for more details). A strong positive relationship was observed between non-native species richness and precipitation (log-transformed) which was significant for the pooled and partially pooled data (Adjusted  $R^2 = 0.2$ ,  $p = 1.49 \times 10^{-8}$  for the pooled data and marginal  $R^2 = 0.17$ ,  $p = 0.003$  for the partially pooled data, Figure 2d). Non-native species richness showed a negative relation to road density only for the pooled data (Adjusted  $R^2 = 0.02$ ,  $p = 0.044$ , Figure 2e).

Mean community niche width had a hump-shaped relationship with elevation (Adjusted  $R^2 = 0.12$ ,  $p < 0.05$  for the pooled and marginal  $R^2 = 0.044$ ,  $p < 0.01$  partially pooled data, Figure 3a, see Table 2 for more details), a positive relationship with precipitation (log-transformed, only for the pooled data, adjusted  $R^2 = 38$ ,  $p < 2 \times 10^{-16}$ , Figure 3d) and a negative relationship with road density (log-transformed, adjusted  $R^2 = 57$ ,  $p < 2 \times 10^{-16}$  for the pooled and marginal  $R^2 = 0.19$ ,  $p = 1.12 \times 10^{-16}$  for the partially pooled data, Figure 3e). Community mean elevational range showed a positive relationship with elevation (adjusted  $R^2 = 49$ ,  $p < 2 \times 10^{-16}$  for the pooled and marginal  $R^2 = 0.47$ ,  $p = 2.26 \times 10^{-5}$  partially pooled data, Figure 3b).

The range of precipitation realized by the individual species showed a pattern of environmental filtering with increasing



**FIGURE 2** (a) Mean community niche width of non-native plant species and (b) mean elevational range versus number of non-native species. Number of non-native species versus (c) mean annual temperature, (d) mean annual precipitation and (e) road density. LM stands for the results from a simple univariate linear regression model using the predictor variable shown in the respective graph (pooled data). The regression line for the LM is shown in dark grey. LME stands for a univariate linear mixed-effects model using the predictor variable shown in the respective graph. The regression lines from a partial pooling LME approach for each transect are shown in the respective colors of the islands. Asterisks indicate level of significance: \* $p < .05$ , \*\* $p < .01$  and \*\*\* $p < .001$ . Solid lines indicate significant relationships, dashed lines non-significant relationships. See Table 2 for results of the corresponding linear mixed effects models using transect ID as random factor

precipitation, i.e., species with broad precipitation ranges (generalists) were more frequent in humid conditions, while precipitation specialists dominated in dry conditions (Figure 4a). In contrast, temperature filtering was not directional but characterized by an optimum temperature range of 10–20°C with temperature-specialist filtering out toward low and high temperatures (Figure 4b). Both, precipitation and temperature filtering observed for the investigated islands are not related to global temperature and precipitation ranges realized by the investigated species (see Figure S4).



**TABLE 2** Model results for a simple linear model and a linear mixed-effect model corresponding to Figures 2, 3, and 6. MAT = Mean annual temperature, MAP = Mean annual precipitation, # Non-native species = Number of non-native species. Transect was used as random effect (slope + intercept) for each model. Marginal  $R^2$ , Conditional  $R^2$ , AIC and  $p$ -values are given. Thereby, the Marginal  $R^2$  is the contribution of variance that is explained by the fixed effect alone and the Conditional  $R^2$  is the variance explained by the fixed effect plus the random effect

Model	Simple linear model			Linear mixed-effect model				Figure
	Adjusted $R^2$	AIC	$p$ -value	Marginal $R^2$	Conditional $R^2$	AIC	$p$ -value	
Mean community niche width ~ # Non-native species	0.07	-477.14	0.001	$4.96 \times 10^{-5}$	0.75	-609.27	0.93	2a
Mean elevational range ~ # Non-native species	0.01	2130.40	0.12	0.077	0.33	2113.64	0.0015	2b
# Non-native species ~ $MAT^2 + MAT$	0.002	918.84	0.51/0.40	0.13	0.63	855.70	0.008/0.002	2c
# Non-native species ~ $\log(MAP)$	0.20	886.51	$1.49 \times 10^{-8}$	0.17	0.34	875.97	0.003	2d
# Non-native species ~ Road density	0.02	915.02	0.044	0.051	0.45	891.41	0.14	2e
Mean community niche width ~ $Elevation^2 + Elevation$	0.12	-484.25	0.037/0.002	0.044	0.80	-649.56	0.007/0.0009	3a
Mean elevational range ~ Elevation	0.49	2036.15	$<2 \times 10^{-16}$	0.47	0.69	2016.91	$2.26 \times 10^{-5}$	3b
Mean community niche width ~ MAT	0.015	-469.47	0.076	0.02	0.84	-641.96	0.15	3c
Mean community niche width ~ $\log(MAP)$	0.38	-535.78	$<2 \times 10^{-16}$	0.083	0.77	-632.16	0.065	3d
Mean community niche width ~ $\log(Road\ density)$	0.57	-588.75	$<2 \times 10^{-16}$	0.19	0.64	-623.08	$1.12 \times 10^{-6}$	3e
Mean community niche width ~ % Anemochory	0.062	-476.55	0.0015	0.014	0.77	-616.61	0.13	6a
Mean community niche width ~ % Anthropochory	-0.004	-466.63	0.54	0.004	0.74	-605.47	0.20	6b
Mean community niche width ~ % Hydrochory	0.081	-479.37	0.0003	0.014	0.70	-608.70	0.019	6c
Mean community niche width ~ % Zoochory	0.031	-471.87	0.019	0.002	0.76	-604.70	0.32	6d

Mean annual precipitation showed a hump-shaped relationship with elevation when accounting for transect and island identity but not for the pooled data (Fig S1a and Table S1 for statistics). MAT showed a strong negative relationship with increasing elevation (for the pooled and partially pooled data, Figure S1b and Table S1 for statistics) and road density decreased with increasing elevation (log-transformed, for pooled and partially pooled data, Figure S1c, Table S1). MAP showed a negative relationship with road density while MAT had a positive correlation with road density (both only for the pooled data, Figure S1d and e, Table S1).

### 3.2 | Dispersal strategies and niche width of non-natives

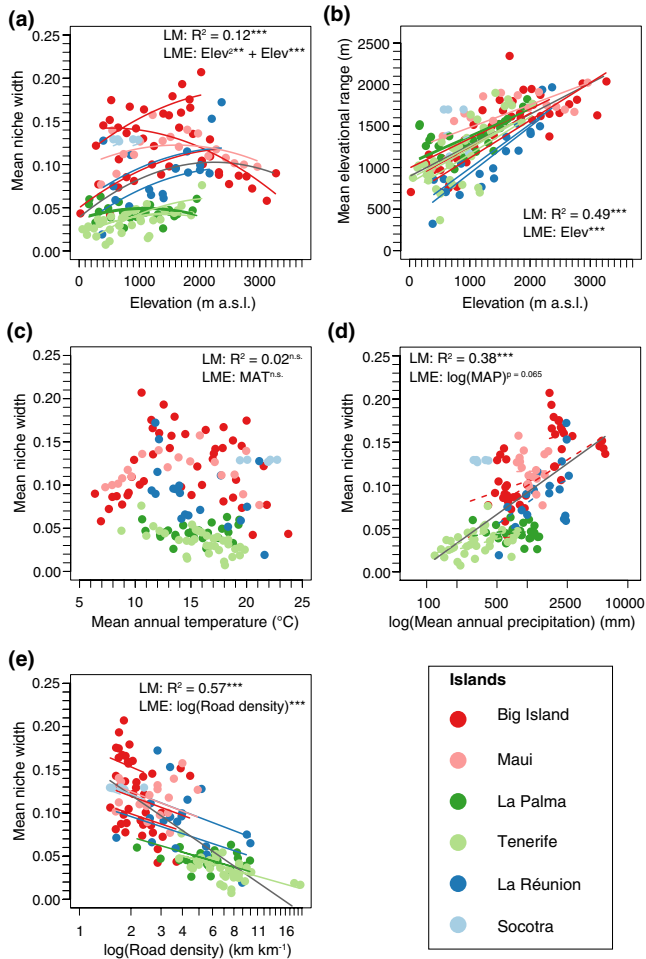
The probability of a species being wind dispersed increased with species-specific niche width (anemochory,  $p = 0.00284$ , Figure 5a). The same was true for probability of a species being dispersed by humans (anthropochory,  $p = 0.0251$ , Figure 5b). However, species niche width showed no significant effect for hydrochory and zoochory ( $p = 0.806$  and  $p = 0.2097$ , respectively, Figure 5c,d). We found

no significant differences for species-specific niche width (i.e., environmental hypervolume, Figure S5a) and elevational range (Figure S5b) between the four dispersal strategies (anemochory, zoochory, hydrochory, and anthropochory;  $p = 0.19$  for both, environmental hypervolume and elevational range).

At the community level, we observed effects of dispersal strategies on the mean community niche width (i.e., hypervolume). Mean community niche width increased with percent anemochory and percent zoochory species in the communities (only for the pooled data, adjusted  $R^2 = 0.062$ ,  $p = 0.0015$ , and adjusted  $R^2 = 0.031$ ,  $p = 0.019$ , respectively, Figure 6a,d) but decreased with percent hydrochory (Adjusted  $R^2 = 0.081$ ,  $p = 0.0003$  for the pooled and marginal  $R^2 = 0.014$ ,  $p = 0.019$  partially pooled data, Figure 6c). Percent anthropochory had no effect on the mean community niche (Figure 6b, Table 2 for statistics).

### 3.3 | Relative importance of climate, human impact and dispersal strategies

Altogether climate, human impact and dispersal strategies explained a substantial proportion variance of mean community niche width



**FIGURE 3** (a) Mean community niche width and (b) mean elevational range of non-native plant species per plot against elevation. Mean community niche width per plot versus (c) mean annual temperature, (d) mean annual precipitation and (e) road density. We calculated mean community niche width by applying a kernel density-based hypervolume approach based on temperature and precipitation regime (see methods for details). LM stands for the results from a simple univariate linear regression model using the predictor variable shown in the respective graph (pooled data). The regression line for the LM is shown in dark grey. LME stands for a univariate linear mixed effects model using the predictor variable shown in the respective graph. The regression lines from a partial pooling LME approach for each transect are shown in the respective colors of the islands. Asterisks indicate level of significance: \* $p < .05$ , \*\* $p < .01$  and \*\*\* for  $p < .001$ . Solid lines indicate significant relationships, dashed lines non-significant relationships. See Table 2 for results of the corresponding linear mixed effects models using transect ID as random factor

( $R^2 = 0.74$ ; Figure 7). The major share of the explained variance was explained by human impact and climatic variables, i.e., the combined effects of MAT, MAP (log-transformed) and road density (human 28% + climate 20% + human/climate 28% = 76% of explained variance). Dispersal strategy was only subordinate in explaining mean community niche width independently (4%), while the jointly explained variance of dispersal strategies and road density amounted to 11% and of all three groups to 8%.

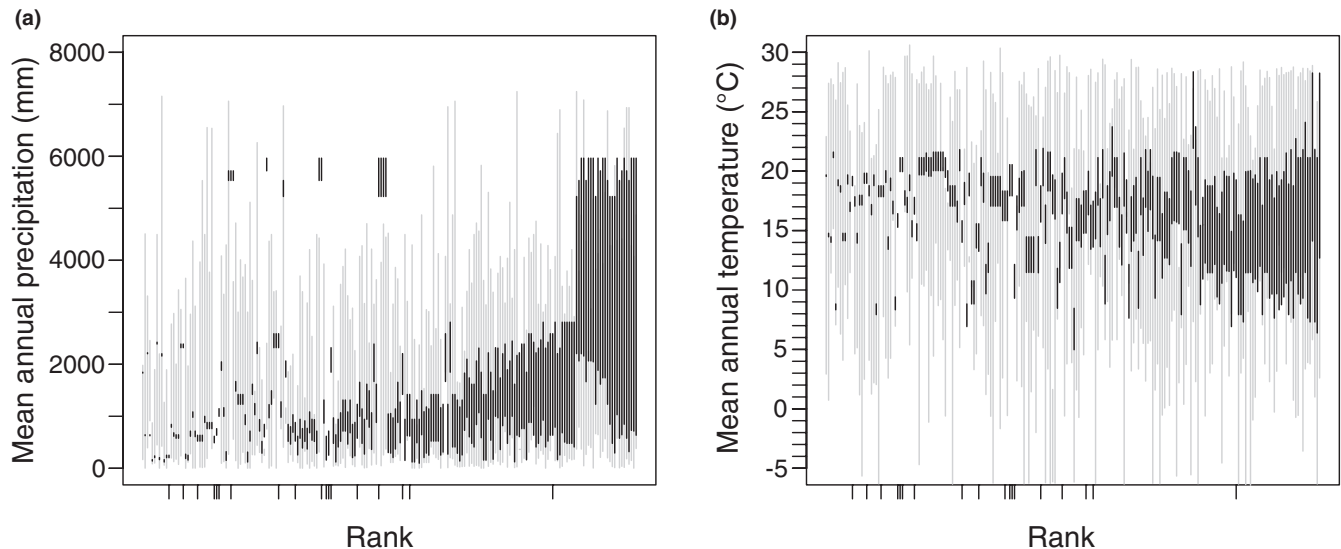
## 4 | DISCUSSION

Our study sets out to understand the major drivers of directional ecological filtering acting on non-native plant species on islands. We use roadside communities spanning elevational gradients on islands distributed in all major oceans in the tropics and subtropics and test the effects of climate, human influence and species dispersal strategy. Although directional ecological filtering, as proposed by Alexander et al., (2011), provides a valuable framework for biological invasions along environmental gradients, our study highlights the importance to look more in detail at the underlying environmental drivers related to climate, human impact and dispersal strategies. First, we confirm that the elevational range of non-native species increases with elevation as proposed by directional ecological filtering (Figure 3b). Second, when looking more in detail at the underlying drivers of directional ecological filtering, we see that precipitation and human impact (i.e., road density) are the main drivers, while temperature that has previously been proposed as a major driver of invasion processes on islands (Arévalo et al., 2005; Daehler, 2005) is of subordinate importance for the ecological amplitude (environmental niche width) of non-native species (Figure 3, Table 2). Third, temperature and precipitation specialists are restricted to areas of moderate-temperature conditions of 10–20°C and low-to-moderately high precipitation values of 100–1500 mm/year (38% of the non-native species in our study fall in this category), while generalist species also occur outside of this corridor (Figure 4, 62% of the non-native species). This supports the optimal environmental window hypothesis of Cury and Roy (1989). Fourth, while dispersal strategy overall has little influence on niche width (Figure 7), we see that generalist species favor specific dispersal strategies (namely anemochory and anthropochory, Figure 5). This indicates that these two dispersal strategies increase species' niche width because they are better adapted to disperse along roads.

### 4.1 | Directional ecological filtering on tropical and subtropical islands

We observed no unidirectional response of species' temperature range along the temperature gradient, but rather a bidirectional effect. Specialists subsequently drop out when moving out of the thermal optimum toward low- as well as high-temperature extremes. The observed pattern with maximum species occurrence in the center of the realized temperature range might be comparable to a mid-domain effect (sensu Colwell & Lees, 2000), where species occurrence is restricted by the limits of the realized temperature conditions. However, we observed a unidirectional, non-linear filtering effect for precipitation with regard to the range of precipitation realized by non-native plant species. For this climatic filter, we observed specialists to occur under low precipitation conditions, which can occur at both ends of the elevational gradient. With increasing precipitation and, thus water availability, also species' precipitations range increase and specialists are increasingly





**FIGURE 4** Range of (a) mean annual precipitation and (b) mean annual temperature realized by non-native plant species on islands. Each species is ranked from narrowest to widest climatic niche on the respective climate gradient. Niche width is here quantified as the range of temperature and precipitation covered by the species on all islands in our study (shown in black). The grey bar indicates for each species the global precipitation and temperature range, respectively. Black ticks indicate species with missing information on global distribution, i.e., global precipitation and temperature niche range

filtered out (see Figures 3d and 4). We find that precipitation is particularly important on the cross-island scale, but also seems to have an ecological relevance on the within-island scale because the slope of all transects is positive in the partial pooling (although strictly speaking not statistically significant, Figure 3d and Table 2). Both, the observed precipitation and temperature filtering are not related to the global temperature and precipitation ranges realized by the investigated species—a fact that reinforces the importance of climatic filtering as a structuring force for non-native plant communities on islands.

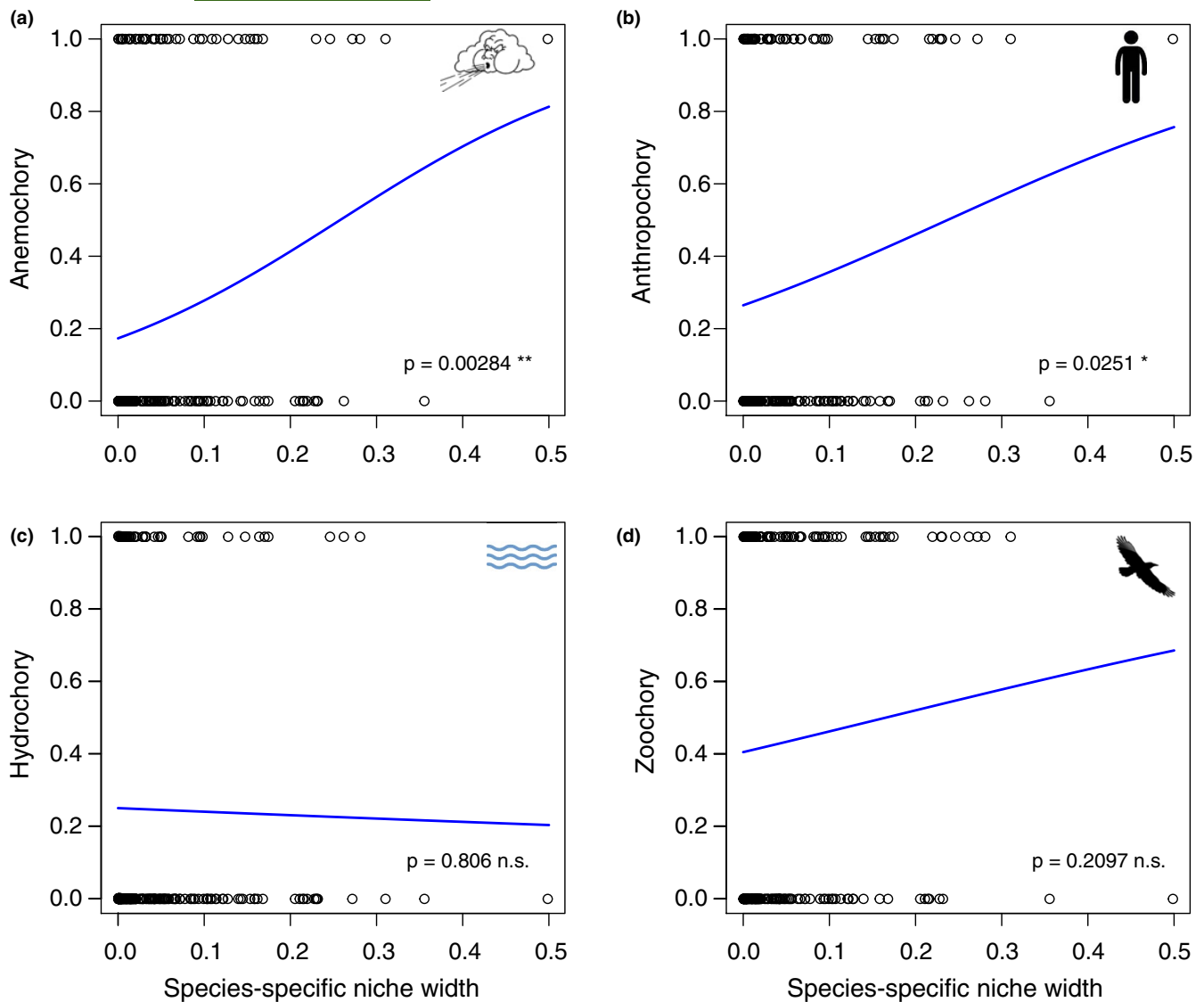
As suggested by Alexander et al., (2011), a thermal filter at low elevations (where most non-natives arrive due to high human impact; Pauchard et al., 2009) leads to a strong negative selection of non-native high elevation specialists, resulting in an effective increase in overall generalism in the arriving non-native species pool. However, human impact (quantified as road density) also had an important impact on structuring the niche width of non-native species. In fact, human impact was the best overall predictor of niche width of non-native species, nearly explaining 1/3 of the explained variance (Figure 7). The local influence of human impact can obviously override climatic filters that might be more dominant on larger scales, by producing site conditions more favorable for non-native species than expected by climate alone (Catford et al., 2011).

Interestingly, our results show that, by taking advantage of the unique climatic conditions of trade wind and monsoonal islands, directional ecological filtering is not driven by temperature but actually by precipitation and human impact on tropical and subtropical islands—an important addition to the theoretical framework proposed by Alexander et al., (2011). Within islands, increasing amounts of precipitation lead to a subsequent dropping out of xerophytic

specialists, while precipitation generalists with a wide tolerance of moisture conditions are not affected.

#### 4.2 | The effect of dispersal strategies on non-native niche width

When looking at the effect of species' dispersal strategies we observed anemochory (dispersal by wind) and anthropochory (dispersal by humans) to be significantly correlated with species' environmental niche width. In other words, species dispersed by wind and humans occupy larger environmental niches on islands than species which do not use these dispersal strategies. In contrast, dispersal by water and animals did not show any effects on non-native niche width. Thus, besides climatic filtering and habitat accessibility (i.e., road density), dispersal by wind and humans seems to be an important driver of niche occupation for non-native species on tropical and subtropical islands. This is in line with von der Lippe and Kowarik (2012) who argue that roadsides offer specific conditions that favor certain types of dispersal strategies that are adapted to wind drag by cars (e.g., small seed size) and other human activities. However, in comparison to climate and human impact, dispersal strategies were the weakest predictor of non-native niche width (Figure 7). This leads to the conclusion that dispersal strategies are only of subordinate importance for plant invasion processes on tropical and subtropical oceanic islands, also because previous studies have shown that the altitudinal limits of non-native species along roadsides are not dispersal limited but rather in equilibrium with their climatic limits (Alexander et al., 2009).



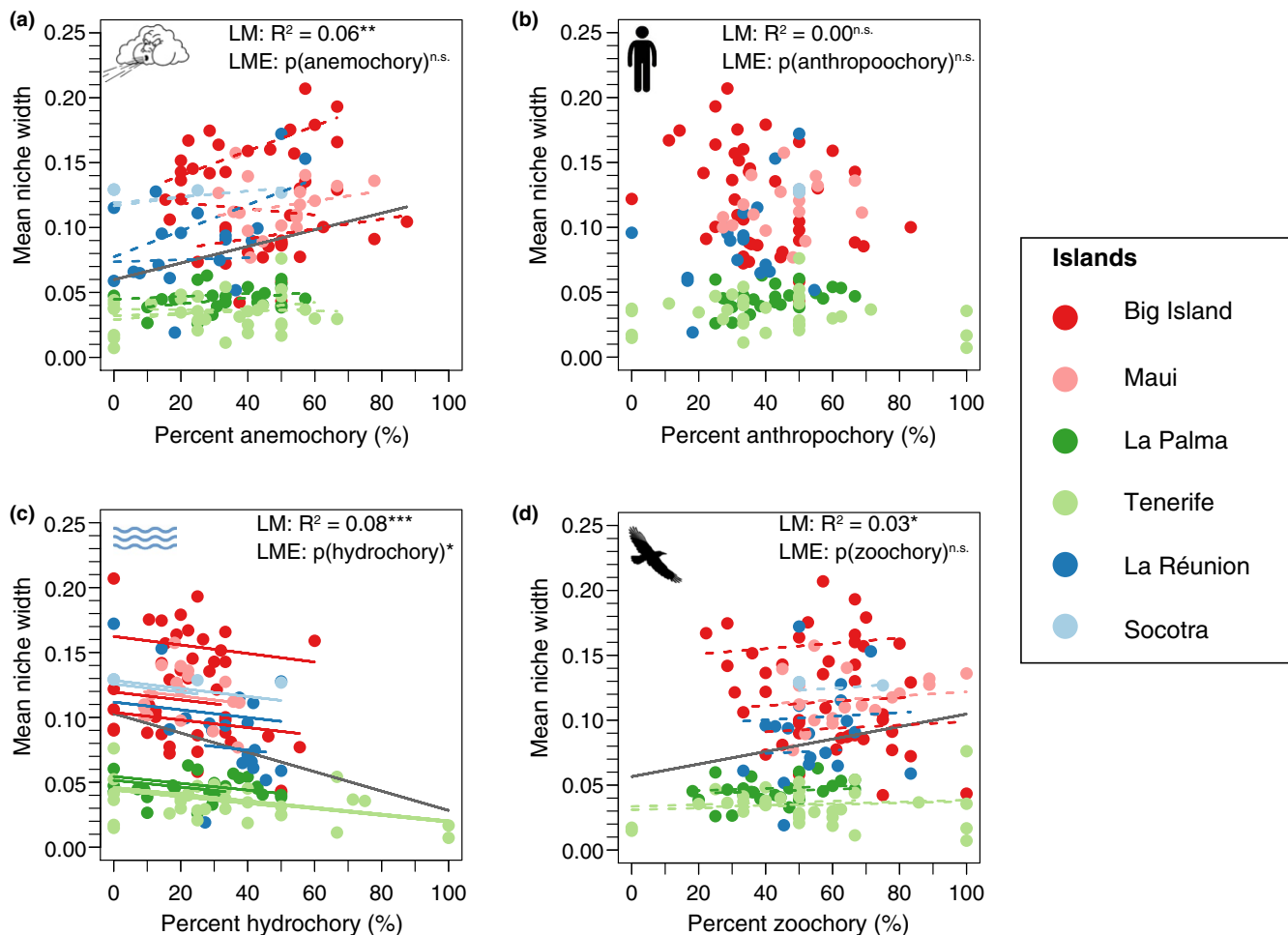
**FIGURE 5** Relationship between dispersal trait occurrence and environmental niche width of the investigated non-native plant species for (a) anemochory, (b) anthropochory, (c) hydrochory and (d) zoochory. Blue lines and  $p$ -values depict the predictions and statistics of generalized linear models with a binomial distribution which were used to test the effects of species niche width (i.e., hypervolume) on the probability of being dispersed by wind, water, animals, and humans, respectively. See full statistical results in Table S6

In general, information on dispersal strategies was more abundant for species with bigger environmental niches (Figure S5c), which might bias our observations to a certain degree. However, the contrasting trends we observed between species-specific niche width and the different dispersal strategies made us rather confident about the ecological significances of these observations, indicating an ecological trend rather than a bias as a result of deficient data.

### 4.3 | Generalists versus specialists

In summary, our results suggest that generalist species are favored by directional ecological filtering because (a) of the higher probability

that species with large environmental niches will randomly overlap with (at least some part of) the main introductory regions at high human impact where introduction probability is high, and (b) once established in these introductory regions generalists can spread within the climate space of the recipient island. This spread seems to be mainly driven by the environmental tolerance of the species in combination with human-mediated habitat accessibility and dispersal. In contrast to generalists, specialists that have established under high human impact conditions, will have a lower probability of spreading into other climatic and human impact conditions found on the recipient island because their environmental requirements are confined to the conditions found at or similar to the conditions of the introductory region.



**FIGURE 6** Effect of four different dispersal strategies on mean community niche width. Dispersal strategies are given in relative contribution per plot (%). We calculated mean community niche width by applying a kernel density-based hypervolume approach based on temperature and precipitation regime (see methods for details). LM stands for the results from a simple univariate linear regression model using the predictor variable shown in the respective graph (pooled data). The regression line for the LM is shown in dark grey. LME stands for a univariate linear mixed effects model using the predictor variable shown in the respective graph. The regression lines from a partial pooling LME approach for each transect are shown in the respective colors of the islands. Asterisks indicate level of significance:  $*p < .05$ ,  $**p < .01$ , and  $***p < .001$ . Solid lines indicate significant relationships, dashed lines non-significant relationships. See Table 2 for results of the corresponding linear mixed effects models using transect ID as random factor

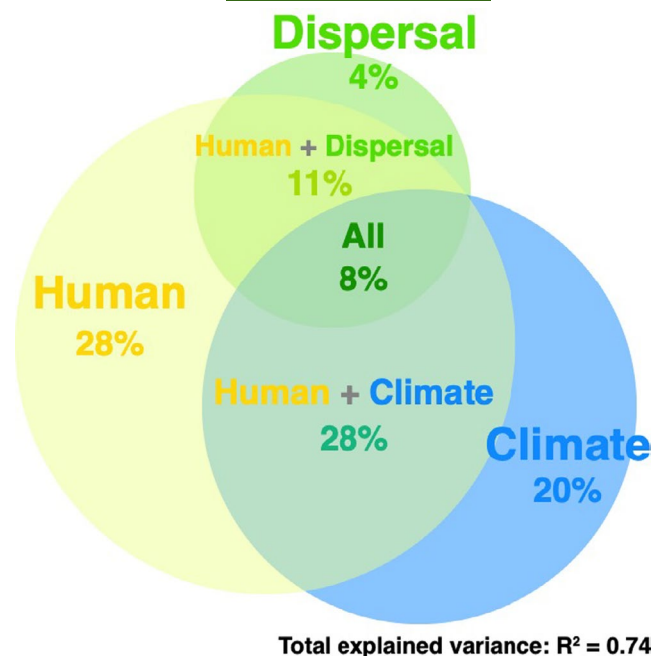
#### 4.4 | Island-specific idiosyncrasies in the observed patterns

By adding elevational transect as random factor to the model, we can explain a substantial portion of variance in niche width of non-native plant species that is not covered by climate or human impact factors as well as dispersal alone. On the one hand, this might have to do with the fact that we used relatively simple climate factors (MAT and MAP) that only describe certain (albeit important) aspects of the climatic conditions affecting plant invasion. Annual means, for example, neglect temporal climate dynamics such as seasonality effects or inter-annual variability, which might additionally influence plant invasion (Parepa et al., 2013) as well as the contribution of fog drip that can be quite substantial in certain locations on trade wind-influenced islands (Ritter et al., 2008). However, the temporally and spatially high-resolution climate data necessary for such

analyses are often insufficient or missing on high elevation islands with complex, small-scale topography where climatic conditions can dramatically change within a few hundred meters—a caveat highlighted by Harter et al., (2015). On the other hand, the factor transect integrates across a wide range of environmental (e.g., indicating if a transect is located on windward or leeward side of an island) and spatial information (spatial proximity of plots along the transect) but also local road conditions (e.g., regarding age, traffic frequency, management, etc.), which are not covered by large-scale climatic or human impact factors.

## 5 | CONCLUSION

The large coverage in global climate space of our islands (Weigelt et al., 2013) suggests that the findings in our study are likely not



**FIGURE 7** Independent and joint variance of mean community niche width of non-native plant species explained by grouped climatic drivers, dispersal strategies and human influence as a result of variance partitioning. The circles and overlap of the Venn diagram are drawn proportionally to scale. The climate group consists of mean annual precipitation (log-transformed) and mean annual temperature, the dispersal group of percent anemochory and percent hydrochory, and human impact is quantified by road density (log-transformed). Non-significant variables were excluded. The independent and joint contribution per group is given as the percentage of the total explained variance

restricted to islands but might be applied to plant invasion phenomena where comparable environmental gradients exist (see Zefferman et al., 2015). Interestingly, our results show that patterns of plant species invasion across islands as well as within-islands can be largely quantified with species–climate and species–human interactions, i.e., human-mediated habitat accessibility, invasibility and dispersal, at least for roadside communities that are often the starting point for invasions into natural habitat (Haider et al., 2018; McDougall et al., 2018). The strong dependence of plant invasion on climatic and human drivers likely means that with ongoing climate change (Harter et al., 2015), interactions with other neobiota (Cubas et al., 2019) and land use change (Caujapé-Castells et al., 2010), plant invasion processes on islands will be strongly affected.

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#### DATA AVAILABILITY STATEMENT

The raw data for all previously unpublished datasets (La Réunion and La Palma) are published in DRYAD Online repository (Irl et al., 2021). All other datasets are cited accordingly. Also, a list of all environmental and anthropogenic variables as well as a list regarding each species status (alien vs native) and dispersal trait is published in DRYAD Online repository (Irl et al., 2021).

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### BIOSKETCH

The author team around Severin D.H. Irl, Andreas H. Schweiger and Anke Jentsch is interested in the mechanisms behind plant invasion. They use the climatic heterogeneity of islands as model systems to better understand plant invasion processes. To make cross-island comparisons possible, the team used a standardized sampling protocol from the Mountain Invasion Research Network (MIREN; <https://www.mountaininvasions.org/>) for most islands.

Author contributions: SDHI, AHS and AJ conceived the ideas; AJ, CAP, JRA, AC, CCD, OF, PM, RO, DS, JMIS and AHS provided the data; AHS analyzed the data; SDHI and AHS lead the writing with a substantial contribution from all authors.

### SUPPORTING INFORMATION

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

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