RESEARCH ARTICLE

Disentangling natural and anthropogenic drivers of native and non-native plant diversity on North Sea islands

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Abstract

Aim: Biodiversity on islands is commonly explained by a set of natural drivers such as area, isolation and habitat heterogeneity. However, constant human impact has led to considerable changes in island floras worldwide. This is reflected, among others, in increased numbers of non-native species. Barrier islands are discrete land units, strongly influenced by humans and not displaying significant evolutionary dynamics. This makes them highly suitable for studying contemporary patterns of species richness and underlying processes. We aim to disentangle the effects of established natural and anthropogenic drivers on native and non-native plant species richness at the example of 31 European barrier islands.

Location: 31 North Sea barrier islands located off the Dutch, German and Danish coast.

Taxon: Native and non-native plant species (spermatophytes and ferns).

Methods: Individual relationships of natural and anthropogenic drivers with native and non-native plant species richness are analysed with generalised linear models (GLMs). We use structural equation models (SEMs) to additionally account for inter-relations between drivers.

Results: Island area was the strongest predictor of native and non-native plant species richness but affected richness mostly indirectly through habitat heterogeneity (non-native species) and island inhabitants (native species). Isolation had a slight negative effect on native and non-native plant species numbers on islands.

Main Conclusions: The richness of native and non-native plant species on islands is associated with different drivers, that is, habitat heterogeneity and island inhabitants respectively. This might be caused by distinct underlying processes forming native and non-native richness patterns. Area was confirmed to be the most important driver of species richness but acting primarily through other natural and anthropogenic drivers of plant species richness. We encourage considering both natural and anthropogenic drivers and their interrelatedness to explain contemporary biogeographic patterns of species richness.

KEYWORDS
alien species, barrier islands, biodiversity, habitat heterogeneity, island biogeography, isolation, nature conservation, SAR, structural-equation model, Wadden Sea

1 | INTRODUCTION

Extensive human impact on islands worldwide challenges the equilibrium theory of island biogeography (MacArthur & Wilson, 1967)—an elegant yet simple model that predicts species richness of discrete land units (e.g. islands). Humans have intentionally and unintentionally altered large parts of biotic as well as abiotic aspects of islands in all oceans (e.g. Fernández-Palacios et al., 2021; Nogué et al., 2021; Rojas-Sandoval et al., 2020; Tordoni et al., 2021). Thus, in times when humans considerably influence islands worldwide (e.g. Gleditsch et al., 2023; Graham et al., 2017; Helmus et al., 2014; Irl et al., 2021; Nogué et al., 2021; Steinbauer & Beierkuhnlein, 2010; Walentowitz et al., 2022), and natural systems are severely under pressure, it is paramount to consider anthropogenic in addition to natural drivers of insular biodiversity to advance our basic understanding of processes generating biodiversity on islands (Gleditsch et al., 2023).

Species numbers on islands have been increasing and are predicted to continue to rise in the future, mainly due to the accidental and deliberate introduction of non-native species (also referred to as alien species) by humans (Sax et al., 2002; Seebens et al., 2017; Walentowitz et al., 2023). In consequence, total plant species richness on some islands has more than doubled, and the number of non-native species exceeds the number of native species (Essl et al., 2019). Additionally, turnover rates increased 9.5-fold with the onset of human settlement on islands, as palaeoecological research, dating back up to 5000 years, revealed (Nogué et al., 2021). The introduction of non-native species even changes fundamental biogeographical relationships such as the species-isolation relationship (Moser et al., 2018). In natural island systems, species numbers predictably decrease with increasing spatial isolation. However, the number of successfully established non-native species increases with spatial isolation. As already predicted from the equilibrium theory (MacArthur & Wilson, 1967), isolation is linked with low species richness of native species and, consequently, increased invasibility (Moser et al., 2018). Human influence supports this process mainly by functioning as a vector of transportation, reducing functional isolation and changing the available area with suitable habitat conditions on islands through land use change.

Hence, it is evident that studies profit from complementing natural biogeographical drivers with anthropogenic drivers when aiming to unveil drivers of contemporary biodiversity. To explain the number of insular non-native species, anthropogenic predictor variables such as the number or density of human inhabitants and tourists (e.g. Essl et al., 2019; McMaster, 2005; Rojas-Sandoval et al., 2020; Walentowitz et al., 2022), human infrastructure such as roads (e.g. Irl et al., 2021; Rojas-Sandoval et al., 2020) or per capita gross domestic product (GDP; e.g., Tordoni et al., 2021; Denslow et al., 2009) have been proven influential. Additionally, the number of native species has been shown to be directly influenced by anthropogenic drivers, such as human population or roads (e.g. Bailey et al., 2017; Rojas-Sandoval et al., 2020). Native plant diversity can additionally be influenced indirectly by human activity through introduced animal and plant species (Luna-Jorquera et al., 2012). The number of native and introduced species (termed naturalised species by the respective study) seem to be directly

related as native richness is an excellent predictor of naturalised plant species (Sax & Gaines, 2008). In most studies, natural biogeographical drivers of species richness, primarily island area and isolation, were shown to have stronger influences on insular species numbers compared to the effects of human activities (e.g. Moody, 2000; Rojas-Sandoval et al., 2020; Tordoni et al., 2021; Walentowitz et al., 2022). Nevertheless, anthropogenic drivers increase the explanatory power of models explaining insular species numbers and with continuing and increasing anthropogenic pressure on islands the importance of these variables can be expected to increase.

A little-acknowledged fact is that island biogeographical theory is rooted in barrier islands (Palmgren, 1915–1917 on Åland archipelago; MacArthur & Wilson, 1967 on the Florida Keys). Barrier islands are highly suitable to exclusively account for species assemblages and underlying processes as these systems are commonly dynamic and short-lived (compared to oceanic islands) and usually do not exhibit evolutionary processes (e.g. speciation) (Niedringhaus et al., 2008). Thus, barrier islands fall perfectly into the domain of the equilibrium theory of island biogeography as missing speciation dynamics of barrier islands and their proximity to the mainland enable unhindered colonisation-extinction dynamics. Since the seminal work on island biogeography theory by MacArthur and Wilson (1967), the valuable contributions of such coastal islands and the characteristics of coastal islands lying in-between oceanic and continental islands have been corroborated by several studies aiming at understanding patterns and processes of species occurrences on islands (Kohn & Walsh, 1994; Scherber et al., 2018). On a gradient between oceanic islands (e.g. Hawaii, Canary Islands, Galapagos) and habitat islands or fragmented pieces of land (e.g. hedges between agricultural fields; a lake amidst terrestrial land), barrier islands, as a particular case of coastal islands, can be regarded as an intermediate system.

The focus of studies in island biogeography on oceanic islands contrasts the global importance of barrier islands. Worldwide, there are more than 2000 barrier islands along the world's coasts, covering more than 20,000 km² of coastline (based on remote sensing images at 30 m resolution; Stutz & Pilkey, 2011). These islands commonly show very dynamic morphologies over time as they are commonly agglomerations of loose sediments and are constantly shaped by tides, waves, wind and extreme events such as storms or storm surges (Zhang, 2016). Compared to oceanic island ontogeny, which operates on geological timeframes of hundreds of thousands or millions of years (Borregaard et al., 2017; Whittaker et al., 2008), barrier islands can change within decades. The proximity to continental areas makes barrier islands more susceptible to anthropogenic disturbances as the vicinity to permanently settled continental areas increases the likelihood of settling on barrier islands nearby. Additionally, barrier islands are attractive for tourism and recreational sports activities. The strong anthropogenic imprint on barrier islands calls for a socio-ecological perspective on insular floristic assemblages.

Along the Dutch, German and Danish coast, a chain of barrier islands is arrayed. Scherber et al. (2018) identified habitat heterogeneity to best explain multidiversity (cross-taxa) on the East Frisian Islands (German coastal islands), and Ferreira-Arruda

et al. ([2022](#)) describe island area and geomorphological changes to best explain plant diversity on these islands. However, the magnitude of influence by anthropogenic drivers and the inter-relation of natural and anthropogenic biogeographical drivers of species richness remain unclear. In this study, we aim to disentangle anthropogenic and natural biogeographic drivers of native and non-native plant species richness at the example of barrier islands located along the Dutch, German and Danish North Sea coasts. Our approach considers natural and anthropogenic drivers and their interrelatedness to challenge a set of hypotheses ([Figure 1](#)) presented in detail in the following sections.

1.1 | Natural drivers

1.1.1 | Area

Area generally emerges as the strongest predictor of species numbers on islands (e.g. Kreft & Jetz, [2007](#); Lomolino, [2000](#); MacArthur & Wilson, [1967](#)). Thus, we expect area to drive both native and non-native plant species richness. As habitat heterogeneity is often highly

Natural   Anthropogenic
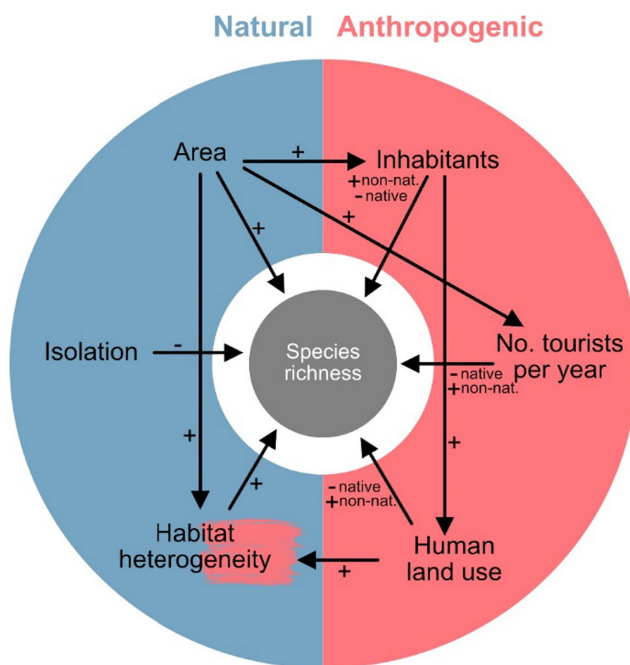
FIGURE 1 Schematic representation of hypothesised relationships between natural biogeographical (blue) and anthropogenic (light red) drivers of native and non-native plant species richness. Richness can be influenced directly (e.g. by area) or indirectly (e.g. larger island area leading to increased habitat heterogeneity that positively influences species richness). Positive relationships are indicated by a plus (+) and negative relationships with a minus (−) and are hypothesised to differ between non-native and native species in the number of inhabitants, tourists and the impact of human land use. Habitat heterogeneity is mainly considered to be a natural driver but can be anthropogenically influenced, hence the colouring in blue and light red.

correlated with area, we subsequently expect area to contribute directly and indirectly (through habitat heterogeneity) to insular species richness (Kohn & Walsh, [1994](#)). We also expect area to influence species richness via the number of inhabitants and tourists, as larger islands will have a higher influx of people which can potentially negatively impact native species richness and lead to increased non-native plant species richness (Denslow et al., [2009](#); Spear et al., [2013](#)).

1.1.2 | Habitat heterogeneity

The higher the diversity of habitats, the more species (native and non-native) can establish due to vacant niches (Hortal et al., [2009](#)). The inclusion of area and habitat heterogeneity, being interrelated, allows testing for the relative roles of spatial processes (area) and niche-related processes (habitat heterogeneity) (Udy et al., [2021](#)). This parameter represents not purely a natural biogeographical driver but can be influenced by human activities.

1.1.3 | Isolation

Often measured as Euclidean distance from an island to the next mainland, is considered the second most relevant driver of species richness for insular species after area and is expected to be negatively related to species richness (MacArthur & Wilson, [1963](#), [1967](#)). For barrier islands, Diver ([2008](#)) used the area of the landmasses surrounding an island to explain species numbers. We, therefore, expect isolation according to Diver ([2008](#)) to be negatively correlated with native species richness on North Sea islands. We also expect non-native species numbers to decrease with increasing isolation as these plants can not only reach the islands via human transport but can also self-disperse from the near mainland, which is highly populated and hosts numerous non-native species.

1.2 | Anthropogenic drivers

1.2.1 | Human land use

We expect native species to be negatively influenced by human land use due to reductions in natural habitat (e.g. Sánchez-Ortiz et al., [2020](#)) and non-native species to be positively affected by this anthropogenic driver as it leads to the creation of novel human-dominated and disturbed habitats for non-native species (e.g. Pretto et al., [2010](#)). Furthermore, habitat heterogeneity is impacted by human land use (Geri et al., [2010](#)).

1.2.2 | Inhabitants

We hypothesise that a larger number of inhabitants affects the number of non-native species by increasing propagule pressure, as has

been previously shown for other systems (Denslow et al., 2009; Spear et al., 2013). Meanwhile, more inhabitants increase the pressure on native habitats and are expected to reduce native species richness. Additionally, the number of inhabitants present on an island is predicted to influence the amount of anthropogenically used land.

1.2.3 | Touristic pressure

Tourism might affect propagule pressure; thus, we expect the number of non-natives to be positively associated with the number of tourists (Dimitrakopoulos et al., 2022). Negative impacts of tourism on native species richness are expected for the same reasons as those expected for inhabitants.

2 | MATERIALS AND METHODS

2.1 | Study area

For this study, 31 islands located along the coast of the Netherlands, Germany (Lower Saxony, Schleswig-Holstein), and Denmark were considered (Figure 2). Of these, 20 are true barrier islands, eight islands have formed around mainland cores ("Geestkerninseln"), and three islands are Halligen (very small marsh islands that are frequently impacted by storm surges). The island Nigehörn is exceptional as it was created artificially through hydraulic filling in 1989. The prevailing wind conditions come from a west-south-westerly direction (Siegismund & Schrum, 2001). The North Sea exhibits areas with microtidal (up to 1.35 m), mesotidal and macrotidal (more than 2.90 m) ranges (Böse et al., 2018; Hayes, 1975).

The Frisian Islands resulted from the dynamic interactions between sea and land and commonly consist of unconsolidated sandy material (Davis, 1994; Wang and Roberts Briggs, 2015). Periodic and aperiodic disturbances lead to a constant relocation of material from west to east (e.g. inlet sedimentation bypassing; Fitzgerald et al., 1984). At the same time, these natural processes are being counteracted by human activities, slowing down or preventing these dynamics by building dikes, relocating tons of sand or greening dunes (de Groot et al., 2017). The Frisian saying "Gott schuf das Meer, der Friese die Küste" (*God created the sea, Frisians created the coast*) illustrates how natural forces predominantly determine local environmental conditions and that coastal environments result from the interplay of natural forces and centuries of anthropogenic management. The islands are popular for real estate with touristic attractions and numerous recreational activities. Land is partly used for agriculture, however, shifting towards increased touristic use in recent decades.

The native habitats are mainly composed of salt marshes and dunes (TMAP, 2017). Plant species occurring in salt marshes are predominantly herbs and are well adapted to a high salt content in the soil (e.g., *Salicornia* spp., *Puccinellia maritima* and *Bolboschoenus maritimus*) (Leuschner & Ellenberg, 2017a). Dune vegetation can vary dramatically depending on the age of the dune and its distance to the sea, where young dunes are dominated by herb species such as *Cakile maritima* and *Elymus farctus*, while more mature dunes can harbour woody species from small shrubs to tall trees (e.g. *Salix repens* and *Betula pubescens*) (Leuschner & Ellenberg, 2017b; TMAP, 2017). Land use on the target islands can be described as rather extensive compared to mainland areas. Meadows with grazing sheep, cattle and horses are common. In areas surrounding and within human settlements, the vegetation is a miscellaneous of opportunistic species such as *Plantago major*, escaped ornamental ones such as *Rosa rugosa*, and economically important crops such as *Triticum aestivum* (Niedringhaus et al., 2008). All 31 islands share similar maritime climatic conditions with mild winters and cool summers with moderate rainfall and strong winds.

The unique Wadden Sea of the Netherlands, Germany and Denmark, with its islands, fauna and flora and special environmental regimes, has been declared a UNESCO World Heritage Site (11,400 km²) in 2009 with an extension in 2014 (UNESCO, 2022). The 14,950 km² of Wadden Sea are protected by a network of 11,950 km² of Nature Reserves (Netherlands, Denmark) and National Parks (Germany) referred to as the Wadden Sea Conservation Area (Common Wadden Sea Secretariat, 2022). The comparable setting of the 31 study islands along the European North Sea coast (Figure 2), combined with their similarity in climate and topography, make them well-fit for island biogeographic studies.

2.2 | Species occurrence data

We compiled plant species (spermatophytes and ferns) lists for the East Frisian Islands (Niedringhaus et al., 2008, considering plants present since 1980), for the West Frisian Island (NDFF, 2015, considering plants since 1990), for the Danish Frisian Islands (Hartvig & Vestergaard, 2015, considering plants since 1992), and the North Frisian Islands (Hellwig, 2018; GBIF, 2020a–g; LLUR, 2020, considering plants since 1995) derived from extensive species survey by experts and complemented with information from the Global Biodiversity Information Facility (GBIF). The species data thus represent the status quo. We automatically extracted species occurrence information from LLUR (2020) using Python (Van Rossum & Drake Jr, 1995) and the *webbot 0.34* package. We standardised the species' names according to Plants of the World Online (2022). Sub-species and varieties were treated on species level. After name standardisation, we obtained a total of 1804 species. We then classified the species as native and non-native according to the species lists if information was provided and additionally used Tamis et al. (2004), Buchwald et al. (2013) and Haeupler and Muer (2007) for status information (in total native = 1105, non-native = 699).

2.3 | Environmental drivers

For all target islands, we gathered and calculated data on island area, isolation and habitat heterogeneity as natural drivers, and island
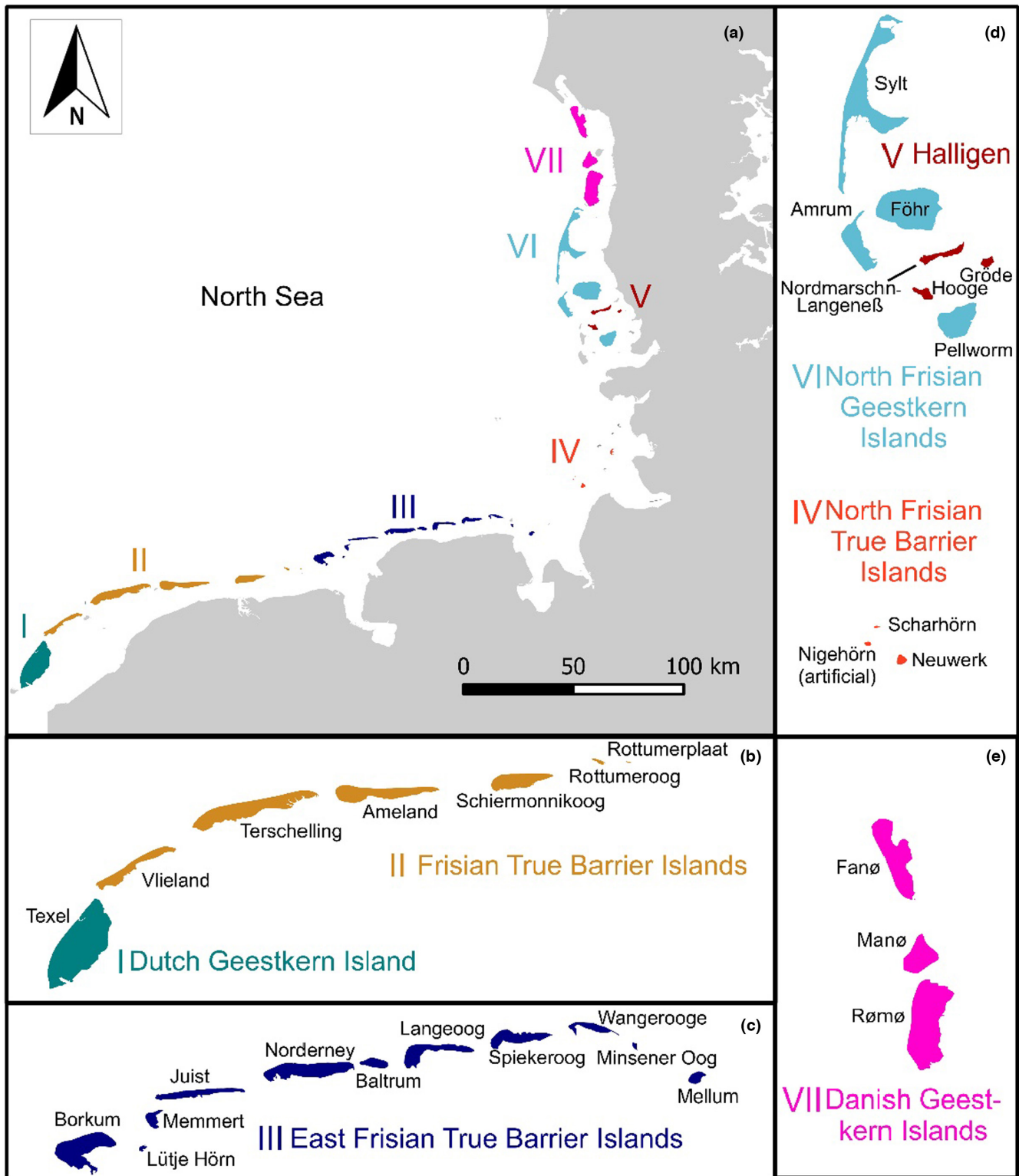
FIGURE 2 Overview of the study area (a) that comprises a total of 31 barrier islands, Geestkern islands, and Halligen along the North Sea coast of the Netherlands (b), Germany (c,d) and Denmark (e).

inhabitants, number of annual tourists and percentage of human land use as anthropogenic drivers (Tables 1; Table S1). We used a landscape measure of isolation (Diver, 2008), for which we calculated the percent land masses (of both neighbouring islands and the mainland) that lie within a buffer around the islands. We calculated

this driver for buffers of 10, 20, 40, 60, 80 and 100km (Figure S1) and selected the buffer showing the highest correlation with native and non-native species richness for final modelling (100km buffer, Table S2). Habitat heterogeneity was calculated by applying the Shannon index (Pielou, 1966) to a total of 24 land use categories

TABLE 1 Natural and anthropogenic drivers used to explain native and non-native plant species richness on 31 North Sea islands.

Driver	Measurement unit
Natural	
Area	km^2
Isolation	Landscape measure of isolation calculated as % land area within a 10, 20, 40, 60, 80 and 100-km buffer zone around the island (sensu Diver, 2008; Figure S1). For the final model building, a buffer of 100 km was chosen, as it showed the highest correlation with species richness (Table S2)
Habitat heterogeneity	Shannon index of 24 CORINE land cover classifications (Land Cover, European Environment Agency, 2013, release from 2018) sensu Scherber et al. (2018)
Anthropogenic	
Inhabitants	Number of inhabitants per island (sources listed in Table S3)
Tourist numbers	Annual number of visiting tourists per island (sources listed in Table S3)
Human land use	% land used anthropogenically based on CORINE Land Cover classifications (European Environment Agency, 2013; selection of classes Table S4)

(CORINE Land Cover, European Environmental Agency, 2013; selection of classes), following Scherber et al. (2018). Island ontogeny, which has been proven to increase the explanatory power of models explaining insular species numbers (Borregaard et al., 2017; Whittaker et al., 2008) was not included in the study as coastal islands are commonly not places of large speciation events and island dynamics have not proven to explain species richness on some of the target barrier islands (Scherber et al., 2018).

The number of inhabitants and tourists visiting the islands per year (during pre-pandemic times) was sourced from a set of administrative and web sources (Table S3). The cover of land significantly altered by humans was calculated as the percentage of land cover units (CORINE Land Cover, European Environmental Agency, 2013) that were identified as anthropogenic land use categories (selection of classes Table S4) per island. We acknowledge that the diversity of non-native plant species on islands has been explained in other studies by socio-economic drivers, such as Gross Domestic Product (GDP) (Kueffer et al., 2010; Wohlwend et al., 2021). However, these studies commonly focus on oceanic islands (Wohlwend et al., 2021) and include islands at larger scales differing in GDP. As our target islands are only partly inhabited and open for tourism, form part of the European Union (EU) and are spatially very close to each other, we did not include GDP as an explanatory variable.

2.4 | Data analysis

We tested the premise that island species numbers are not biased due to differences in island ontogeny (i.e. true barrier island, Geestkern island, Hallig) or affiliation to different countries with an ANOVA and post-hoc Tukey HSD. For the main analysis, we chose two approaches (uni- and multivariate) applied to the same dataset to shed light on the data from different angles, which is valuable when dealing with complex ecological data. Data analysis and visualisation were conducted in R Version 4.0.5 (R Core Team, 2022). Univariate relationships between insular native and non-native

species richness and natural and anthropogenic drivers were assessed by fitting generalised linear models (GLMs; Poisson family error, log link). GLMs containing anthropogenic variables were limited to inhabited islands. When fit, log-transformed variables were used for GLMs to increase model performance (assessed by Akaike Information Criterion, AIC). Model fit of GLMs was evaluated by analysing the distribution of the residuals. Pseudo R^2-values were calculated according to Nagelkerke (1991) using the package *rms* (Harrell Jr, 2020). Additionally, GLMs were built using standardised species richness values (standardised to max = 1) to compare slopes between models describing native and non-native species richness.

Additionally, we fit structural equation models (SEM) (Grace, 2006; Shipley, 2016) to distinguish how different natural and anthropogenic drivers jointly affect native and non-native plant diversity, respectively, and to account for interrelations of drivers according to our set of hypotheses (Figure 1). The advantage of SEMs is that they allow the measurement of direct and indirect effects and give account to the complexity of a system. SEMs were built based on a correlation matrix of all drivers that showed a significant univariate relationship with native and non-native plant species richness based on univariate GLMs, using the *lavaan* package (Rosseel, 2012; Table S5). Multivariate normality was assessed using the *MVN* package (Korkmaz et al., 2014) to ensure that model requirements concerning data distribution (skewedness, kurtosis) are met. Accordingly, if necessary, drivers were log- or square root-transformed to meet the requirement of normal data distribution. Model fit was evaluated by ensuring that the degrees of freedom are positive and do not exceed $n(n+1)/2$, with n = number of observed variables. Additionally, we report Chi-square, root mean square error of approximation (RMSEA), standardised root mean square residual (SRMR), non-normed fit index (NNFI) and comparative fit index (CFI) to evaluate the overall model fit (Fan et al., 2016; Table S6). For visualisation, non-significant paths were removed to receive the most parsimonious model. As the anthropogenic drivers are expected to strongly influence models with values of zero for non-inhabited islands, we repeated the SEMs using a subset of only inhabited islands.

3 | RESULTS

With 1060 species, the westernmost and largest of all studied islands, Texel, exhibited the highest plant species richness, including the highest number of native ($n=824$) and non-native ($n=236$) species (Table S1). The uninhabited East Frisian Island Lütje Hörn exhibited the lowest species number ($n=66$), of which only five species were non-native and 61 species were native. Lütje Hörn also represented the smallest of the target islands. On Sylt, the highest percentage of non-native plant species was present (25.7%) while Rottumeroog showed the lowest percentage of such species (7.3%, Table S1). Species richness did not differ significantly between islands affiliated with different countries (Figure S2). The number of species was significantly lower on Halligen, as these islands are commonly smaller than true barrier and Geestkern islands (Figure S3).

On inhabited islands, a mean of 14% of the species was non-native, while on uninhabited islands, this value was lower, reaching a mean of only 9%.

The univariate analysis revealed that native and non-native insular species richness responded strongly to island area (log–log space, $p < 0.001$, Pseudo-$R^2 = 0.60$ and 0.73 respectively), isolation (calculated as the land area within a 100 km radius around the islands, $p < 0.001$, Pseudo-$R^2 = 0.30$ and 0.32 respectively) and habitat heterogeneity ($p < 0.001$, Pseudo-$R^2 = 0.71$ and 0.67, respectively, Figure 3). The slope describing the relationship between standardised richness values and habitat heterogeneity was similar for native and non-native species but differed slightly for area (non-native species richness increased faster with increasing area) and isolation (non-native species richness decreased faster with increasing isolation, Figure S4a–c). From the set of anthropogenic variables,
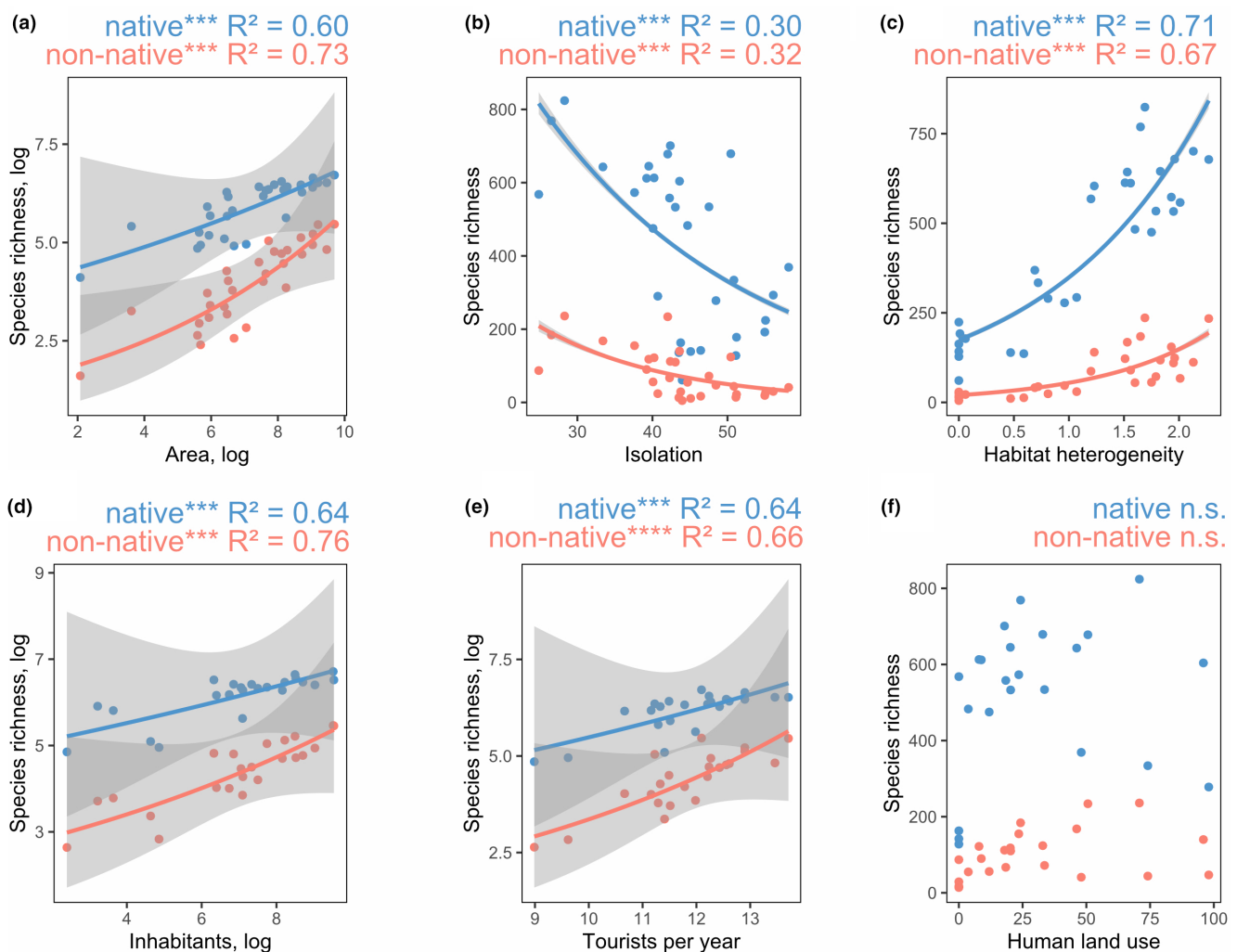

FIGURE 3 The univariate relationships of native (blue) and non-native (light red) insular species richness with area (log-transformed; a), isolation (b), habitat heterogeneity (c), inhabitants (log-transformed; d), tourists per year (log-transformed; e), and the percentage of human land use (f) resulting from GLMs (Poisson family error, log link). Note that the GLMs for the relationship between species richness and anthropogenic variables (d–f) were limited to inhabited islands. Grey-shaded areas indicate confidence intervals of 95% and significance levels are reported using asterisks. Note that the confidence interval in (b) and (c) is very narrow and thus hardly visible. Pseudo-R^2, according to Nagelkerke (1991), is given for significant relationships.

we found that an increase in inhabitants ($p < 0.01$ and $p < 0.001$, Pseudo-$R^2 = 0.64$ and 0.76, respectively, Figure 3d) and the number of tourists visiting annually ($p < 0.01$ and $p < 0.001$, Pseudo-$R^2 = 0.64$ and 0.66, respectively, Figure 3e) led to higher species richness of native and non-native species on inhabited islands. On those islands, human land use did not explain patterns of native and non-native species richness ($p > 0.05$, Figure 3f). Non-native species richness increased faster compared to native species richness with increases of all three anthropogenic variables (Figure S4d–f).

From the joined and interrelated analysis of natural and anthropogenic drivers potentially affecting insular plant species richness with SEMs, we can derive that incorporating driver interrelatedness adds considerable information on the processes that lead to species assemblages on the target islands (Figure 4 and Table S7). Island area drives native plant species richness indirectly by affecting habitat heterogeneity (standardised model estimate of 0.7) and inhabitants (standardised model estimate of 0.8), which explains large amounts of the variety in plant species between islands (Figure 4a). Area drives non-native plant species richness primarily by influencing the number of inhabitants (standardised model estimate 0.8) and tourists (standardised model estimate 0.8) which directly impact non-native plant species numbers (Figure 4b). Isolation negatively affects native and non-native plant species richness on inhabited islands (standardised model estimate −0.2). In sum, the direct influence of habitat heterogeneity (standardised model estimate 0.5) and inhabitants (standardised model estimate 0.2) on all islands and isolation on inhabited islands (standardised model estimate −0.2), and the indirect influence of island area on habitat heterogeneity (standardised model estimate 0.7) accounted for large parts of the variation in native plant species richness ($R^2 = 0.88$). The number of island inhabitants (standardised model estimate 0.6) and annual tourists (standardised model estimate 0.3) directly, island area indirectly through the number of inhabitants (standardised model estimate 0.8) per island and tourists visits (standardised model estimate 0.8), and isolation directly (standardised model estimate −0.2, only on inhabited islands) accounted for most of the variation in non-native plant species ($R^2 = 0.88$).

4 | DISCUSSION

Both natural biogeographic and anthropogenic drivers explained large parts of the variance in native and non-native plant species richness on North Sea islands. Multivariate analysis of species richness patterns revealed a complex network of interrelated drivers of species richness and offered insights into the emergence of extant insular richness patterns. European coastal islands offer an excellent natural setting for testing hypotheses in island biogeography (e.g. Scherber et al., 2018 for East Frisian Islands; Ferreira-Arruda et al., 2022 for Dutch and East Frisian Islands). All islands exhibit comparable climatic conditions and distances to the terrestrial mainland. Formation and isolation occurred during the Holocene, leaving no options for idiosyncrasies caused by speciation processes. Besides
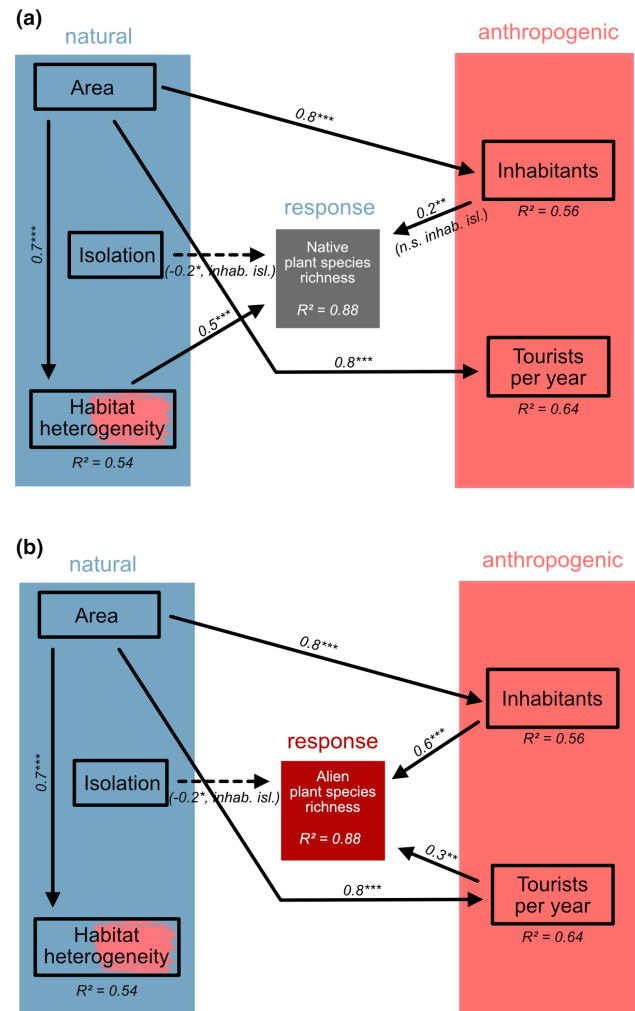
FIGURE 4 Structural Equation Models of natural (blue) and anthropogenic (red) drivers explaining the numbers of (a) native and (b) non-native species present on 31 North Sea islands. Standardised model estimates, significance levels (with asterisks) and R^2-values are given. Dashed arrows indicate results based on a SEMs reduced to inhabited islands ($n = 26$) for those relationships that differed from the full model in significance.

this general homogenous setting, we could identify differences in native and non-native insular plant species numbers that can be explained by a distinct set of drivers.

Univariate analysis revealed that island size was positively related to both native and non-native plant species richness and explained the largest variance of species richness on islands, which aligns with numerous studies in island biogeography (e.g. Kreft et al., 2008; Lomolino, 1982; MacArthur & Wilson, 1967; Triantis et al., 2012). For the East Frisian Islands, representing a subset of our target islands, Scherber et al. (2018) identified area as the second most important driver of overall species richness (plants and animals) after habitat heterogeneity. However, the SEMs suggest area to have an indirect effect on species richness through habitat heterogeneity and inhabitants for native plants and through island inhabitants and tourists for non-native species. In fact, native species richness was

mostly directly driven by habitat heterogeneity, which aligns with Udy et al. (2021) who found this relationship globally. Thus niche-related processes seem to be the prominent underlying cause of native richness patterns in contrast to pure spatial processes (Udy et al., 2021). Conversely to Wohlwend et al. (2021), who identified area and island altitude (which relates to the 3-dimensional area of islands) to explain a large variance of naturalised species richness in the Pacific region, our SEMs suggest no direct effect of this natural biogeographical driver on non-native plants.

According to Scherber et al. (2018), habitat diversity best explained cross-taxa diversity in the East Frisian Islands, representing a subset of this study's target islands. While the univariate analysis resulted in habitat heterogeneity explaining 71% of the variance in native and 67% of the variance in non-native species, the SEMs showed that, in contrast to this general finding and to our expectations, habitat heterogeneity was not relevant in explaining insular non-native plant species richness. The high correlation of several drivers can evoke the impression of an existing relationship and the effects of single drivers can better be assessed by simultaneous application in a model. The detachment of non-native plants from habitat heterogeneity can be explained by the fact that many non-native plants on islands are often ornamentals. This aligns well with a lower percentage of non-native plants found on uninhabited islands compared to inhabited islands in this study. Non-natives thrive within the proximity of humans but would not necessarily resist the hostile conditions close to the sea where sandy soils prevail, and tides, strong winds and salt spray only allow the survival of well-adapted plants. Nevertheless, the relation of non-native plants with habitat heterogeneity has been little explored, as richness patterns are rarely investigated separately for native and non-native species. Scherber et al. (2018), for example, did not differentiate between native and non-native species richness on the East Frisian Islands, and hidden patterns remain veiled. Studies like those by Rojas-Sandoval et al. (2020) and Tordoni et al. (2021) analyse patterns of native and non-native plants separately but do not consider habitat heterogeneity as a driver. The impact of habitat heterogeneity on plant species richness is also difficult to understand, as this driver is in its essence natural, but it can be significantly altered by anthropogenic impact. Additionally, plant population can also be diminished and impacted within natural habitats by human collection (Norton et al., 1994) or browsing, grazing and trampling by non-native animals. To be considered as well is that for non-native plants, environmental filtering might be more critical than dispersal filtering. This point is also stressed by the little importance that isolation played in explaining native and non-native plant species richness on islands. Only a slight negative impact of isolation can be recovered for native and non-native species in the multivariate analyses and univariate analysis. The minor relevance of isolation for near-shore continental islands compared to oceanic islands has been reported before (Weigelt & Kreft, 2013) where it is attributed to the proximity of such islands to source populations. For the analysed coastal islands, the inverse species-isolation relationship reported from remote

oceanic islands by Moser et al. (2018) cannot be confirmed, which can most likely be attributed to the proximity to the mainland and the very different characteristics of the here targeted coastal islands compared to remote tropical and subtropical islands addressed by Moser et al. (2018).

Interestingly, the amount of human land use per island was irrelevant for native and non-native plant species richness. We propose that native species might be unaffected by this anthropogenic driver as firstly, those plants might ostensibly be limited by the prevailing environmental conditions, that is, the influence of strong winds, salt spray and floodings and secondly, human land use is comparatively extensive on the target islands and thus native species persist on anthropogenically used land. Thus, species occurrences might be similar inside and outside anthropogenically used areas. Additionally, some native species on North Sea barrier islands could also be synanthropic, profiting from human land use, which could compensate for a potential loss in numbers of native species in areas under human land use. This could lead to unaffected species numbers but increased turnover and has, to our knowledge, not yet been investigated for the North Sea islands targeted in this study. The reasons for the non-existence of a relationship between human land use and non-native species remain unknown.

The number of inhabitants best explained non-native species numbers on islands which can be seen as a proxy for human activities supporting the establishment of non-natives (e.g. by laying out gardens) or as a proxy for functional connectivity as humans tend to travel between the neighbouring mainland and the islands. Humans most likely function as vectors for such species and directly and indirectly introduce species that then become established on the island. This aligns with literature that confirms the positive influence of human population size and density on the number of non-native species (Denslow et al., 2009; Spear et al., 2013). For the same reasons, the number of tourists was expected to influence the number of non-native species, which was confirmed by both, the univariate and multivariate analyses. The SEMs suggest that the relationship of native species richness with the number of tourists is negligible in this case study. In contrast to non-native species, the number of native species was unaffected by the annual number of visiting tourists, but a slight influence of inhabitants could be recovered. Potential explanations are that firstly, the flora of the North Sea barrier islands is dominated by halophytes (Niedringhaus et al., 2008) and these species are well adapted to the harsh prevailing environmental near-shore conditions where human influence is marginal. Secondly, all islands are located within national parks (Common Wadden Sea Secretariat, 2022), which reduces anthropogenic pressure. The trilateral Wadden Sea agreement between the Netherlands, Denmark and Germany has created a common framework of conservation policies and management to treat the whole Wadden Sea as one entity (Common Wadden Sea Secretariat, 2022). The unaffectedness of native species numbers by tourists could imply that management and protection concept are effective. Additionally, native species might face an extinction debt and the direct effect of, for example,

inhabitants and tourists on the one hand, and plant (and animal) invasions on the other hand might only become effective in the future (Cronk, 2016; Gilbert & Levine, 2013; Otto et al., 2017).

Although we could explain large parts of the variation in native and non-native plant species richness on North Sea islands, additional drivers that we did not consider in our models might be influential, such as the time span of human settlement. Additionally, the border between natural and anthropogenic drivers might be blurry as drivers commonly considered as 'natural' might be anthropogenically impacted. Parts of an island can be uninhabitable for certain species, reducing the effective area they could occupy that can differ from the total area of an island. The effect of island isolation can be reduced by anthropogenic activities that function as vectors, thereby shortening biogeographical distances between islands and mainland areas. In addition to the six focal natural and anthropogenic biogeographical drivers, differences in species numbers between islands might also be attributable to slightly differing survey periods (Aggemyr & Cousins, 2012; Chiarucci et al., 2017), location along geographical gradients (Hawkins & Diniz-Filho, 2004), flooding frequency and intensity and therefrom resulting soil salinity. However, as species richness on true barrier islands did not differ markedly from those on Geestkerninseln (islands with mainland cores) between which soil properties differ, such island characteristics did not seem to influence species patterns significantly. Only Halligen proved to host a lower number of plant species, which can be attributed to their smaller sizes compared to the other target islands.

Biogeographical and biodiversity research is complex considering the multitude of influential natural drivers, and numerous additional anthropogenic drivers that are, in addition, highly interrelated. A recently proposed shortfall of biodiversity research is the *Hookerian* shortfall which delineates that our understanding of human-mediated changes in insular biodiversity is limited (Carine & Menezes de Sequeira, 2020). The shortfall was named after Joseph Dalton Hooker, who demonstrated in the 19th century at the example of the islands Madeira and St. Helena that humans have already massively influenced the flora on those islands and that differentiating between anthropogenic changes and natural processes is challenging. He also identified islands to be well-suited to disentangle natural processes from anthropogenic influences. Our study on the Frisian Islands can be seen as a contribution to tackle this challenge and contribute to a better understanding of the emergence of biodiversity patterns in the Anthropocene.

Our aim was to disentangle the effects of natural and anthropogenic drivers on native and non-native plant species richness on islands while accounting for the interdependency of contrasting drivers at the example of 31 North Sea islands. The double analysis approach (GLMs and SEMs) we chose had the advantage that we could illuminate our data from different sides. Such an approach is well-suited for ecological data as these are often complex and can be ambiguous. The North Sea islands serve well as an example system to challenge and develop theories in island biogeography, especially in the context of anthropogenic influences on biogeographic patterns. We could show that insular native and non-native plant species can be governed by different drivers (natives responded mostly to habitat heterogeneity; non-natives to the number of inhabitants). In general, the research landscape on anthropogenic drivers of insular species richness is growing (e.g. Dimitrakopoulos et al., 2022; Irl et al., 2021; Rodgers III & Parker, 2003; Rojas-Sandoval et al., 2020; Tordoni et al., 2021; Wohlwend et al., 2021). The interrelation of anthropogenic and biogeographic factors that drive species richness patterns should be considered when evaluating the importance of human impacts on species richness patterns for both native and non-native plant species richness (e.g. Gleditsch et al., 2023).

CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Data are openly available on Zenodo (https://doi.org/10.5281/zenodo.8371245) and provided in the Supporting Information.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.