



Socio-Ecological Effects on the Patterns of Non-native Plant Distributions on Hainan Island

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Specialty section:

This article was submitted to
Urban Ecology,
a section of the journal
Frontiers in Ecology and Evolution

Received: 18 December 2021

Accepted: 03 February 2022

Published: 03 March 2022

Citation:

Guo L-Y, Nizamani MM, Harris AJ,
Lin Q-W, Balfour K, Da L-J, Qureshi S
and Wang H-F (2022)
Socio-Ecological Effects on
the Patterns of Non-native Plant
Distributions on Hainan Island.
Front. Ecol. Evol. 10:838591.
doi: 10.3389/fevo.2022.838591

Non-native plants spread to recipient areas via natural or human-mediated modes of dispersal, and, if the non-native species are invasive, introduction potentially causes impacts on native plants and local ecosystems as well as economic losses. Therefore, we studied the diversity and distributional patterns of non-native plant species diversity in the tropical island province of Hainan, China and its relationships with environmental and socioeconomic factors by generating a checklist of species and subsequently performing an analysis of phylogenetic diversity. To generate the checklist, we began with the available, relevant literature representing 19 administrative units of Hainan and determined the casual, naturalized, or invasive status of each species by conducting field surveys within 14 administrative units. We found that non-native plants of Hainan comprise 77 casual species, 42 naturalized species, and 63 invasive species. Moreover, we found that non-native plant species had diverse origins from North and South America, Africa, and Asia and that the most common species across administrative areas belong to the plant families Asteraceae and Fabaceae. Moreover, the numbers of non-native species distributed in the areas of Hainan bordering the coast are greater than those within interior areas of the province. Among the coastal areas, Haikou has the highest species richness and, simultaneously, the highest values for significantly, positively correlated predictor variables, population and GDP ($R^2 = 0.60$, $P < 0.01$; $R^2 = 0.64$, $P < 0.01$, respectively). In contrast, the landlocked administrative units of Tunchang and Ding'an have the smallest number of non-native species, while their populations are less than a quarter of that of Haikou and their GDP less than one tenth. Among natural environmental variables, we determined that the number of non-native species had the strongest correlation with the minimum temperature in the coldest month, which predicts a smaller number of non-native species. Additionally, non-native species are primarily distributed in urban and rural

built-up areas and agricultural areas; areas that are dominated by human activities. Overall, our study provides a working checklist of the non-native plants of Hainan as well as a theoretical framework and reference for the control of invasive plants of the province.

Keywords: biodiversity, invasive plants, species richness, biogeography, urban green space, phylogenetic diversity, flora of Hainan

INTRODUCTION

Non-native species invasions have emerged as a major global environmental and economic issue (Liu et al., 2017; Xiong et al., 2018; Ju et al., 2020; Zhou et al., 2020) and are one of the leading causes of biodiversity loss worldwide (Guo et al., 2020). Therefore, studying non-native species, including potential invasives, is important for understanding their local diversity and distributions. The diversity and distributions of non-native species are known to be driven by socio-economic variables, which influence the time and pathways for and number of species to be introduced to recipient locations, and by natural environmental variables, which affect how many species are able to persist in these new locations (Kull et al., 2011; Tassin and Kull, 2015; Blackburn et al., 2016; Early et al., 2016; Dyer et al., 2017; Vaz et al., 2017; Bellard et al., 2018). With respect to invasive species specifically, their diversity and distributions are often attributable to extensive worldwide trade and transportation (Sardain et al., 2019), although cultural preferences for non-native species that happen to be invasive are also an underlying cause (Wang et al., 2011; Schelhas et al., 2021). Introduction of potentially invasive species often relies on economic and social activities, so wealthier and more populated countries or local areas may accidentally or deliberately import more invasive species (Zhai et al., 2018). Moreover, for all non-native species, including invasives, the environmental conditions of the native range can often accurately predict the invaded range (Wang et al., 2011; Beans et al., 2012). In particular, temperature and precipitation affect the distribution of non-native plants; specifically extreme cold and limited precipitation have a negative impact on non-native species richness (Beans et al., 2012). Previous studies have usually only focused on the impact of either natural environmental or socio-economic variables on the diversity and distribution of non-native plants. In contrast, our study, as explained below, comprehensively considers both types of variables as potential driving forces of the diversity and distributional patterns of non-native plants within the Chinese island province of Hainan.

Hainan boasts a tropical climate and lush forests that are rich in animal and plant diversity (Nunes Leonel et al., 2020) and is one of the most valuable biodiversity conservation areas in China (Zhang, 1998; IUCN, 2013; Wang et al., 2016). Hainan is economically strategically located between the mainland and Pacific Ocean and is an important maritime channel for China to connect with Southeast Asia and other regions (Cheng et al., 2021). Thus, Hainan has been at the forefront of Chinese economic policy reform (Central Committee of the Communist Party of China, and National Assembly of the

PRC, 2018, 2020; NPC Standing Committee, 2021) and is home to a major port within China's Belt and Road project (China National Development and Reform Commission et al., 2015). This project, and the construction of free trade ports in recent years, has promoted considerable foreign trade within Hainan. Moreover, Hainan attracts many domestic and foreign tourists (Lin, 2021), with 76,273,900 tourists visiting in 2018; an increase of 13.08% from 2017. The tourism revenue during this period was approximately 950.16 billion Yuan, an increase of 17.14% from the previous year (Hainan Provincial Bureau of Statistics, 2019). Trade and tourism are known to be positively correlated with non-native species, especially invasive; for example, ore trade increases the risk of plant invasions by sea and commercial vehicles (Lin et al., 2021), and patterns of tourism impact the arrival of invasive species intentionally and accidentally via the travel choices of visitors (González et al., 2008).

The introduction of non-native species to Hainan increases the risk of species invasions. The most current island-wide studies of non-native species are Shan and Wang (2011), who reported 140 species in 82 genera (see also Shan, 2003; Shan et al., 2006), and Peng et al. (2013), who reported 158 non-native plant species in 39 families and 117 genera. However, these previous studies neither clarified the invasive status of each non-native plant species nor inferred the driving forces behind their distributional patterns.

In this study, we compiled a comprehensive list of non-native plant species for each administrative unit (city or county) within Hainan based on field surveys and data from existing literature, and we used the list to gather molecular sequence data and perform an analysis of phylogenetic diversity. Within our study we addressed two main questions: (1) How are non-native plant species distributed across Hainan, and (2) What are the main socio-economic and natural environmental factors affecting their distributional? We especially sought to provide information for resource managers and policymakers to guide their efforts to limit the spread of invasive species on Hainan, and our work may have implications for other tropical islands, which are understudied in terms of non-native species distributions and plant species invasions (Fridley et al., 2007).

MATERIALS AND METHODS

Definition of Terms

In this study, we categorized "non-native" species as those species that are not necessarily inherently dangerous but have spread beyond their native range or are being widely introduced into a new area. Non-native species are also sometimes called foreign

species, alien species, and non-indigenous species (Jeschke and Strayer, 2005). We further divided non-native species into casual, invasive, and naturalized species. Among these, “casual” species as those that do not have self-replacing populations (Booth et al., 2003), while “naturalized” species are those that reproduce and maintain non-native populations without direct human interference, often producing abundant offspring typically in close proximity to parent plants, but largely lacking the ability to invade existing natural or semi-natural vegetation (Richardson et al., 2010). We use the term “invasive” to refer to non-native species that have all the characteristics of naturalized species but can also spread widely and/or quickly within natural areas and that have adverse effects, such as causing obvious damage or posing potential threats to natural habitats, ecosystems, and/or the economy (IUCN, 2013; McNeely, 2013). The term invasive species is similar to “transformers” or “weeds” as defined by Richardson et al. (2000) and Pyšek et al. (2003).

Checklist of Non-native Species Literature and Database Sources

To develop a comprehensive list of the non-native vascular flora of Hainan, we first used relevant literature and national databases. We obtained papers from Scopus¹ from October 2020 to May 2021 using the search terms “Hainan non-native species,” “Hainan invasive species,” and “Hainan Flora.” We also reviewed major regional floristic works, especially the Flora of China (Flora of China Editorial Committee, 2018) and the Flora Reipublicae Popularis Sinicae (Ma and Clemants, 2006), floras of the nearby provinces of Taiwan and Hong Kong (Li, 1975; South China Botanical Garden of Chinese Academy of Sciences and Hong Kong Herbarium, 2007–2011), and related references (e.g., Shan et al., 2006; Hu et al., 2011; Zhang and Xing, 2011; Ma et al., 2013; Peng et al., 2013; Yang et al., 2015). Moreover, we obtained a list of non-native plant species list for Hainan from China’s knowledge-base website,² which is a key national research service led by Tsinghua University and supported by the People’s Republic of China Ministry of Education, the People’s Republic of China Ministry of Science, the Chinese Communist Party’s Propaganda Department, and the People’s Republic of China General Administration of Press and Publication. For each non-native species among all sources, we determined its invasive status using authoritative lists or compendiums, especially China’s non-native species list (Ministry of Environmental Protection, the People’s Republic of China [MEP-PRC], 2014), the Global Invasive Species Database,³ and the Global Compendium of Weeds.⁴ Species were also inferred as invasive in Hainan if they were listed as invasive elsewhere in the world. For casual and naturalized species, we determined their status based on fieldwork (see below). After obtaining and curating data from these sources, we performed taxonomic

reconciliation based on the backbone taxonomy of the China Natural Herbarium.⁵

Hainan is divided into 19 administrative units. For these administrative units, we used the initial survey data from literature and database sources to determine the presence or absence of each non-native plant species, and we performed fieldwork for 14 of these: Haikou, Sanya, Wuzhishan, Wenchang, Qionghai, Wanning, Chengmai, Danzhou, Dongfang, Ledong, Qiongzong, Baoting, Lingshui, and Changjiang (Figure 1). We conducted fieldwork from November 2015 to July 2016 at sites primarily along Hainan’s major, highly trafficked roadways, including along West Line Road (G225), Middle Road (G224), Dart Road (S304), East Road (G223), and Western High-Speed Road (G98). At these sites, we consulted local experts to learn the locations of populations of non-native species and completed surveys within vegetation plots (see the section “Field Survey Methods” of “Materials and Methods”).

Field Survey Methods

We selected vegetation plots representative of local plant diversity and richness. We examined potential sites based on conversations with local people, or walked several transects from the road to assess the local vegetation and ultimately to find an area for a plot with high species richness. Each vegetation plot comprised one large tree plot (20 m × 20 m) containing five shrub plots (5 m × 5 m) and five plots for sampling both herbs and vines (1 m × 1 m). The shrub, herb and vine plots were located at the four corners and center of the tree plot. We followed the Food and Agriculture Organization of the United Nations to define trees, shrubs, vines, and herbs. In brief, trees are woody perennial plants with a single main stem and a more-or-less distinct crown. Shrubs are woody perennial plants lacking a distinct crown and usually with heights between 0.5 and 5 m. We did not encounter species polymorphic for the tree and shrub habit. Vines are plants with relatively slender stems that can climb, creep, or trail, but cannot grow upright on their own and must be attached to other things to achieve height (FAO, 1998, 2004; UNECE/FAO, 2000). Herbs are all other vascular plant species and are usually annuals. Within plots, we identified species according to the backbone taxonomy of the China Natural Herbarium (see text footnote 5), and checked them against our non-native species list. Although our field work did not include late summer to early autumn months, the seasonal change in tropical Hainan is limited and is not expected to affect the presence or absence of plant species.

In addition to establishing and surveying field plots, we also consulted with residents and experts to determine whether certain populations of non-native species were self-reproducing. If they were, we considered these species to be naturalized instead of casual. Our consultations with locals and our observations in the field allowed us to designate some of the naturalized species as “tentatively” or “potentially” invasive (i.e., species that grow faster and have a wider habitat distribution, which indirectly affects the growth of other plants through competition, causing damage to local habitats or ecosystems) in Hainan, but these species had no negative impacts elsewhere in the world according to the

¹<https://www.scopus.com/home.uri>

²www.cnki.net

³www.issg.org/database

⁴www.hear.org/gcw/

⁵www.cfh.ac.cn

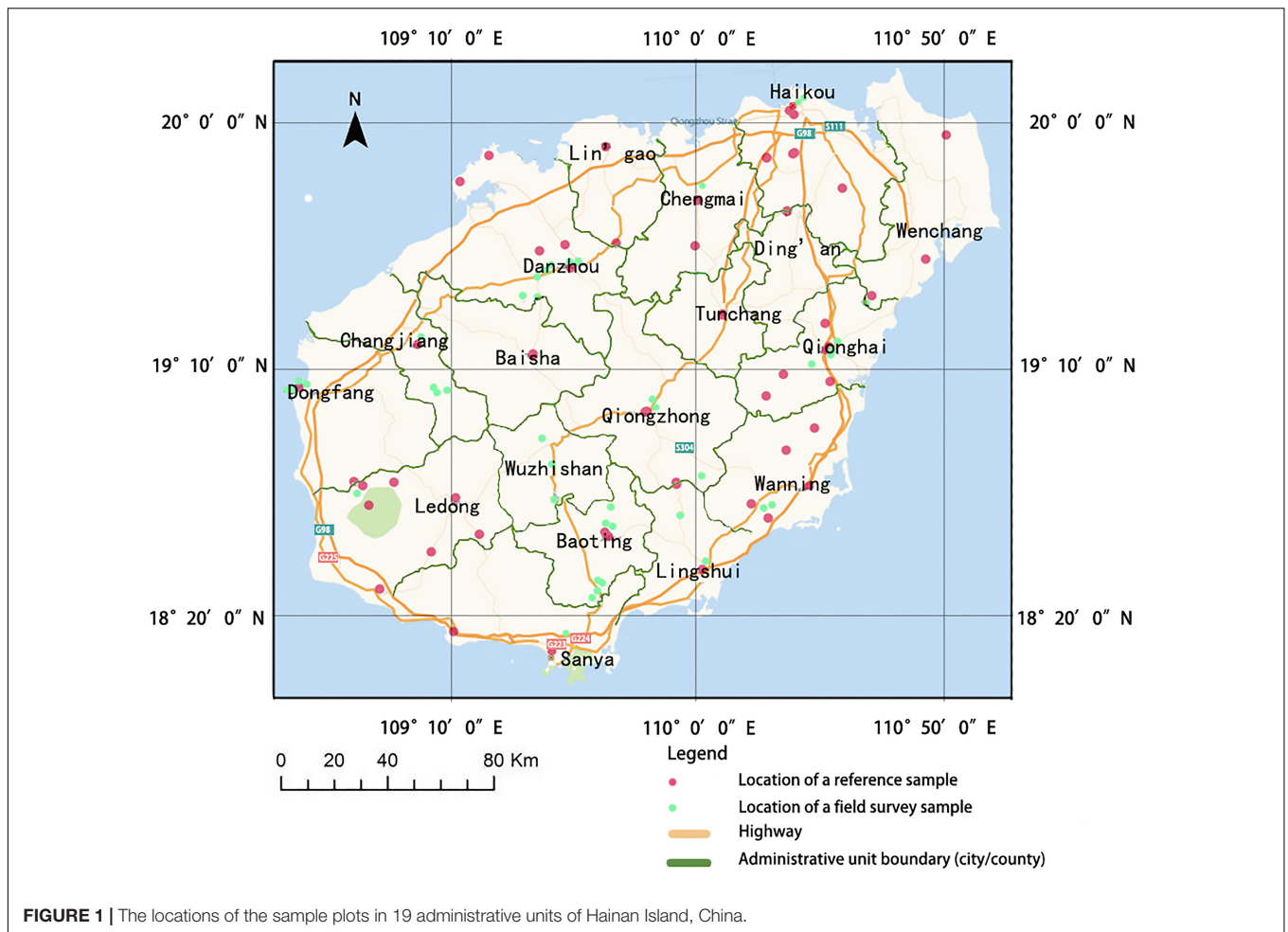


FIGURE 1 | The locations of the sample plots in 19 administrative units of Hainan Island, China.

literature. Nevertheless, the magnitude and extent of the impacts of these species (either environmental or economically) were not assessed in this study and merit further research.

Ultimately, our fieldwork yielded a vetted list of non-native species and their status as casual, naturalized, or invasive within 14 of 19 administrative units of Hainan. We also obtained the distribution of non-native plants in the remaining five administrative units and their status as naturalized, casual, or invasive from the literature (see above). To determine whether biogeographic structures exist in the organization of plant families or plants with different growth habits in urban landscapes, and to attempt to examine the distribution and abundance of non-native species in different habitat types and their assemblages based on geographic and climatic sources, we determined the following information for each species: (i) plant family affiliation, (ii) annual, biennial, or perennial habit, (iii) habitat, (iv) native range, and (v) native climate zone. For plant family affiliation, we followed the taxonomy of Flora of China (Flora of China Editorial Committee, 2018), and to determine if a species was annual, biennial, or perennial, we used Baidu Encyclopedia (<https://baike.baidu.com>). We determined the native ranges of species using the Germplasm Resources Information Network (GRIN) of the United States Department of

Agriculture (www.ars-grin.gov), Wiersema and León (2016), and the Flora of China (Flora of China Editorial Committee, 2018), assigning species ranges by continental areas: Asia, Europe, North America, South America, Africa, Oceania, and unknown native range. Asia and Europe were split by the Ural Mountains, while Oceania comprised mainland Australia and many islands. For habitats, we followed Wang et al. (2011), who based habitat classification on the Flora of China (Flora of China Editorial Committee, 2018), but also accounted for human influence. Habitats were (1) urban and rural built-up areas (i.e., places with many human-made structures), (2) agricultural areas, (3) grasslands and shrublands, (4) forests and forest margins, (5) inland rocky outcrops, (6) inland wetlands and other water bodies, and (7) coastal areas. Using land survey results from a governmental data sharing platform,⁶ we obtained the area of each type of habitat within Hainan and its percentage of the total land area (**Table 1**). This data is mainly derived from the Second National Land Change Survey and the 2010–2016 National Land Change Survey, using the national standard of the People's Republic of China "Classification of Land Use Status."

⁶<http://tddc.mnr.gov.cn/>

TABLE 1 | The area and percentage of total area of each habitat, and the numbers and percentages of non-native and invasive species within each habitat.

Habitats	Area (km ²)	Non-native species		Casual species		Naturalized species		Invasive species	
		N	%	N	%	N	%	N	%
Urban and rural built-up areas (i.e., places with many human-made structures)	0.23 × 10 ⁴	113	62.09%	48	63.16%	21	50.00%	18	66.67%
Agricultural areas	1.67 × 10 ⁴	87	47.80%	29	38.16%	14	33.33%	17	62.96%
Grasslands and shrub lands	0.05 × 10 ⁴	163	1.43%	32	42.11%	22	52.38%	15	55.56%
Forest and forest margins	1.21 × 10 ⁴	144	35.02%	23	30.26%	11	26.19%	5	18.52%
Inland rocky outcrops	0.01 × 10 ⁴	66	0.35%	8	10.53%	5	11.90%	7	25.93%
Inland wetlands and water bodies	0.15 × 10 ⁴	67	4.43%	20	26.32%	9	21.43%	15	55.56%
Coastal areas	0.13 × 10 ⁴	9	3.82%	2	2.63%	1	2.38%	2	7.41%

N, number of species.

Socioeconomic and Natural Environmental Variables

To examine the drivers of geographic patterns of non-native species in Hainan, we investigated their distributional relationships to several socio-economic and natural environmental variables. To quantify the distributions of species we used our species list supplemented with field data and converted this to a presence/absence matrix for each of the 19 administrative units. For socio-economic variables, we measured (i) human population size, (ii) total agricultural revenue in 2013, (iii) industry revenue in 2013, (iv) total retail sales of social consumer goods for 2013, (v) number of tourists in 2013, (vi) bank deposits from residents in 2013, and (vii) GDP in 2013 for each administrative unit. We obtained these data from the Hainan Provincial Bureau of Statistics (2014), and we selected these variables because they are among the most important socio-economic determinates of non-native plant distributions globally (Sharma et al., 2010; Zhou et al., 2020; Gruber et al., 2021).

For natural environmental variables, we selected five variables of the Bioclim2 dataset from the WorldClim database,⁷ Data from this dataset represent averages over 30 years from 1970–2000 (Fick and Hijmans, 2017). For 19 administrative units, we obtained the following environmental variables: (1) minimum temperature of the coldest month (BIO6), (2) maximum temperature of the warmest month (BIO5), (3) mean temperature of the warmest quarter (BIO10), (4) mean temperature of the coldest quarter (BIO11), and (5) mean annual precipitation (BIO12). These variables are known to be key to determining land plant distributions (Harris et al., 2017; Cheval et al., 2020; Li et al., 2020; Xie et al., 2021; Zhu et al., 2021). Moreover, due to the well-known relationship between species diversity and area (Arrhenius, 1921; Barkman, 1989; Zhou et al., 2020), we also obtained land area data (km²). For all natural environmental variables, we acquired data at 30 arc second resolution, and for all variables including land area, we extracted values using ArcMap 10.8.

Analytical Methods

To measure the non-native plant diversity of each administrative unit, we used species richness as well as three metrics for each unit based on the phylogeny of species within each unit. These indices were: Faith's phylogenetic diversity (PD), which is the sum of all phylogenetic distances, or branch lengths, within a phylogenetic tree; phylogenetic mean pairwise distance (MPD), which represents the mean distance between all possible pairs of species within a tree; and phylogenetic mean nearest taxon distance (MNTD), which is the mean distance between each species and its closest relative within the tree (Faith, 1992; Tucker et al., 2016). While PD is a measure of total diversity within a tree, MPD is more sensitive to diversity among deep nodes and MNTD is more sensitive to diversity at the tips.

⁷<http://www.worldclim.org>

For the measures of phylogenetic diversity, we constructed a phylogenetic tree including all vascular species and the non-native species in each administrative unit using the R package “V.PhyloMaker” (Jin and Qian, 2019), which can generate very large phylogenies for vascular plants, and we visualized the result in FigTree v1.4.4. In order to compare phylogenetic metrics between the 19 administrative units, we sought to generate indices that were independent of species richness. Thus, we compared the observed values of PD, MPD, and MNTD to their expected values under a null model using respective standardized effect sizes (ses) following Pavoine and Bonsall (2010): PD.ses, MPD.ses, and MNTD.ses. We conducted these analyses for all non-native species combined and invasive species. Naturalized and casual species have not shown their harm to the ecological environment, so we do not use PD.ses, MPD.ses, and MNTD.ses to evaluate their functional ecological traits. We generated the null models in the R package “picante” using the `phylosor.rnd` function to simulate 999 random assemblages, in which taxa were randomly assigned to the 19 administrative units with species richness and frequency maintained among units (Webb, 2010).

To identify outliers in species richness and the phylogenetic metrics of plant diversity, we calculated *z*-scores for all dependent variables (including the number of non-native, casual, invasive and naturalized species, PD, MPD.ses, and MNTD.ses of non-native and invasive species) in Microsoft Excel 2016. We regarded outliers as those values with a *z*-score greater than 3.0 or less than -3.0 following Kreyszig (1979). After we removed the outliers, we analyzed the relationship of species richness (SR) to the selected socio-economic and climatic variables (see above) as well as land area using linear models (LMs) with step-by-step selection in R (R Development Core Team, 2016). Finally, we selected the best model using the Akaike Information Criterion (AIC). We also built single factor regression models for SR, PD.ses, MPD.ses, and MNTD.ses of non-native species and socioeconomic environmental variables for each administrative unit.

We used the R package “circlize” (Gu et al., 2014) to draw chord diagrams to visualize (1) the relationships between the habitat, native range, and administrative units where the non-native species occur, and (2) the relationships between the habitat, native range, and the nine plant families with the largest numbers of non-native species. We used Jenks natural breaks in IBM SPSS Statistics 23.0 to determine that these nine families have statistically more non-native species in Hainan than other families. We used the K-means algorithm in IBM SPSS Statistics 23.0 to cluster the nine families into groups according to their representation within each administrative unit, and we show the families with the greatest representation in Figure 2.

RESULTS

The Non-native Flora of Hainan

We found a total of 182 non-native vascular plant species belonging to 45 families within Hainan according to our literature and field surveys. Of these species, 77 were casual, 42 were naturalized, and 63 were invasive, while 135 species were

herbs, ten were trees, 27 were shrubs, and ten were vines (Supplementary Appendix 1 “Species list”). Additionally, among the non-native species of Hainan, 76 species are annual, two are biennial, 90 are perennial, five are annual or biennial, seven are annual or perennial, and two species are biennial or perennial. Representative images of some non-native plant species of Hainan are shown in Figure 3.

The climatic origins of non-native, casual, invasive, and naturalized plant species in Hainan Province are mainly tropical and subtropical (Figure 4 and Supplementary Appendix 1 “_Climate zone”). We found that non-native plants were distributed throughout all seven habitat categories inconsistently with the representation of the habitats on the landscape. Specifically, urban and rural built-up areas, agricultural areas, and forests and forest margins account for the largest percentages of the land area of Hainan, while non-native species have the highest occurrence rates in grasslands and shrub lands and forests and forest margins at 89.56 and 79.12%, respectively (Table 1). Among non-native species taken together, 26.92% appear in only one habitat, but only 14.81% of invasive species appear in only one habitat (Table 2). Except for some non-native species with unknown native ranges, the non-native species found in Hainan originate from all continents except Antarctica, but are most frequently native to South America (35.93%), North America (30.37%), and Asia (21.98%) (Figure 5 and Supplementary Appendix 1).

In Hainan, the most common plant families in terms of non-native species richness were Fabaceae, Asteraceae, Euphorbiaceae, Poaceae, and Amaranthaceae, which accounted for 47.80% of all non-native species in total. Many species of Asteraceae and Fabaceae comes from North and South America, while many Amaranthaceae derived from South America. The species of Asteraceae, Euphorbiaceae, Poaceae, and Fabaceae mainly grow in rural and urban habitats and grasslands and shrublands in Hainan (Figures 5, 6).

The Distributional Patterns of Non-native Plants Within Each Administrative Unit

We determined the number of non-native species in each administrative unit as well as their status as naturalized, casual, or invasive (Figure 7). Haikou had the highest number of non-native (109), casual (49), invasive (43), and naturalized (17) species, while Tunchang had the lowest for each (55, 20, 27, and eight, respectively) (Figure 7, 8 and Supplementary Appendix 1).

Overall, the frequencies of habitat types and geographic origins of non-native species are rather consistent across the 19 administrative units (Figure 6). In terms of the distribution pattern of each non-native plant family, Asteraceae is widely distributed and has more species in each administrative unit (Figure 2), e.g., *Mikania micrantha* (Asteraceae) occurs in 10 administrative units in Hainan while members of Fabaceae are dominant non-native species in all administrative units except Wuzhishan according to our analyses using K means (Figure 2).

The PD of non-native and invasive species mirrors SR by showing the highest values in Haikou (Tables 3, 4). With

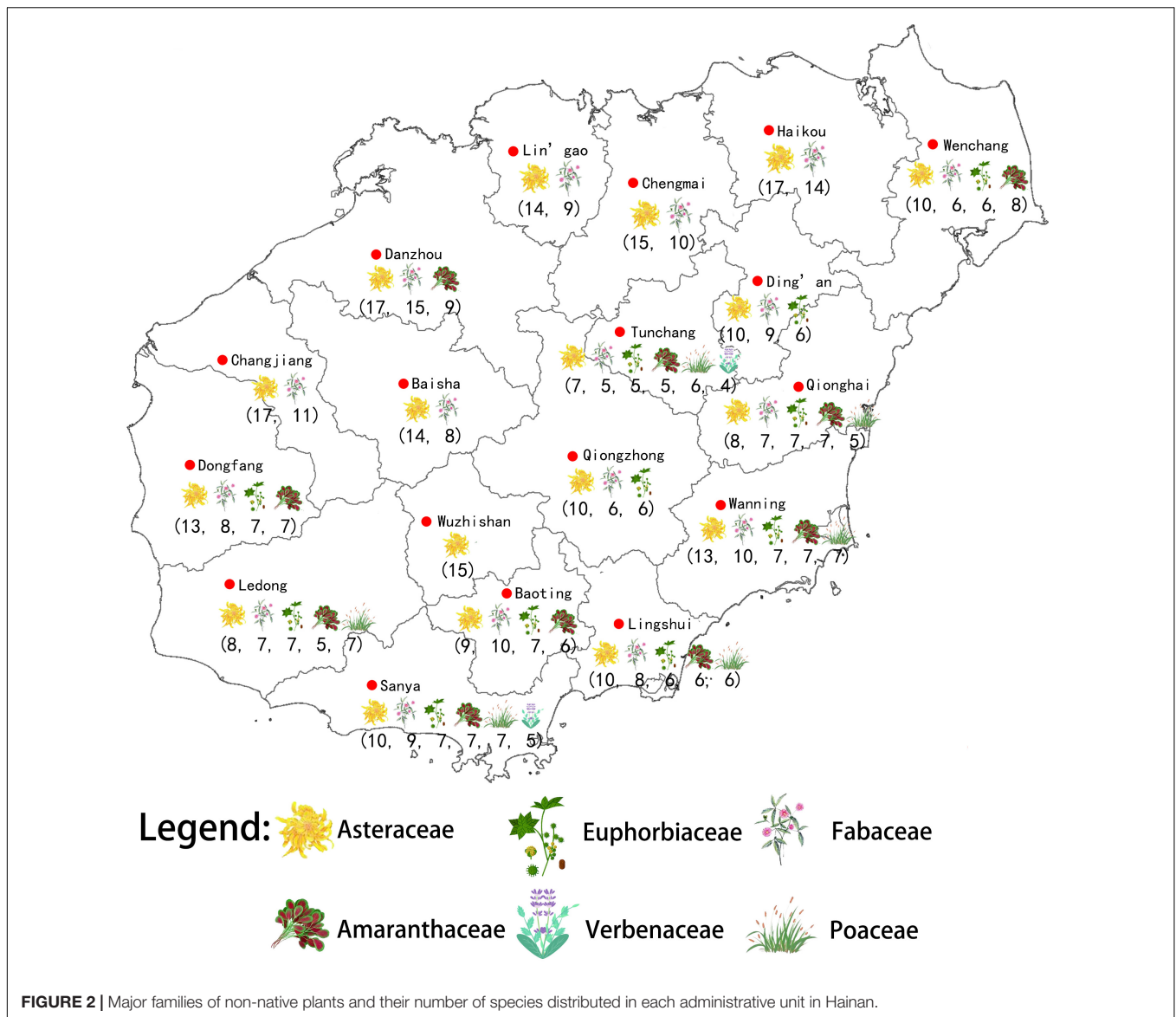


FIGURE 2 | Major families of non-native plants and their number of species distributed in each administrative unit in Hainan.

respect to MPD.ses (Table 3), values showed significant deep phylogenetic clustering ($p \leq 0.05$) for Lin'gao, Danzhou, and Changjiang (Table 3), which are all adjacent to one another along the northwestern coast of Hainan (Figure 1). Among these, the lowest negative value was for Danzhou. Values of MNTD.ses (Table 3) showed significant clustering in Danzhou and Chengmai, which is located geographically between Lin'gao and Haikou (Figure 1). When considering only invasive species (Table 4), no values of MPD.ses or MNTD.ses showed significant phylogenetic clustering or overdispersion.

The Factors Affecting the Patterns of Distributions of Non-native Plants in Hainan

Based on multiple LMs, we found that, among socio-economic variables, GDP and savings deposits in 2013 were significantly

positively correlated with non-native SR (Table 5). Based on simple LMs, we found that, among socio-economic variables, population, total output value of industry in 2013, total retail sales of social consumer goods, savings deposits in 2013, and GDP were significantly positively correlated with non-native, casual, invasive, and naturalized species richness (Table 6). Among climatic variables, the minimum temperature of the coldest month is negatively correlated with the number of non-native, casual, invasive, and naturalized species (Table 6).

The relationship of socio-economic and climate variables as well as land area to phylogenetic diversity is shown in Table 5. We examined the curvilinear relationship between area and non-native species diversity and we found that they were not correlated (Supplementary Appendix 4). According to multiple LMs, the PD of non-native species has a significant positive correlation with land area and GDP. The PD of invasive species



has a negative correlation with Mean temperature of warmest quarter (Table 5). The MPD.ses and MNTD.ses of non-native and invasive species are positive correlated with savings deposits in 2013 (Table 5). The MPD.ses and MNTD.ses of invasive species are positively correlated with mean temperature of coldest quarter (Bio11) (Table 5).

DISCUSSION

Distribution Patterns of Non-native Species in Hainan

Our study used SR and PD to assess the biodiversity of non-native plants. PD is regarded as a highly useful metric of biodiversity for green infrastructure planning and biodiversity conservation strategies in urban ecosystems (Cadotte et al., 2012;

Lopez et al., 2018; Cui et al., 2019), especially because it is a proxy for functional diversity (Knapp et al., 2008; Hooper and Dukes, 2010). Specifically, closely related species are often more similar to each other in terms of functional ecological traits than more distantly related ones (Hooper and Dukes, 2010; Chen and Li, 2018). In Hainan, herbs represent the most common type of non-native plant vascular plant species, and the majority of these are annual herbs. Consistent with previous studies of non-native plant families within the province (Shan, 2003; Shan et al., 2006; Zhang and Xing, 2011; Peng et al., 2013), herbs primarily represent Fabaceae, Asteraceae, Poaceae, Euphorbiaceae, and Amaranthaceae. Thus, although the herbaceous habit is distributed throughout the vascular plant tree of life, the non-native herbs of Hainan are concentrated within a few families, as is consistent with our finding that the non-native herbs in Hainan are distributed in 37 families, and

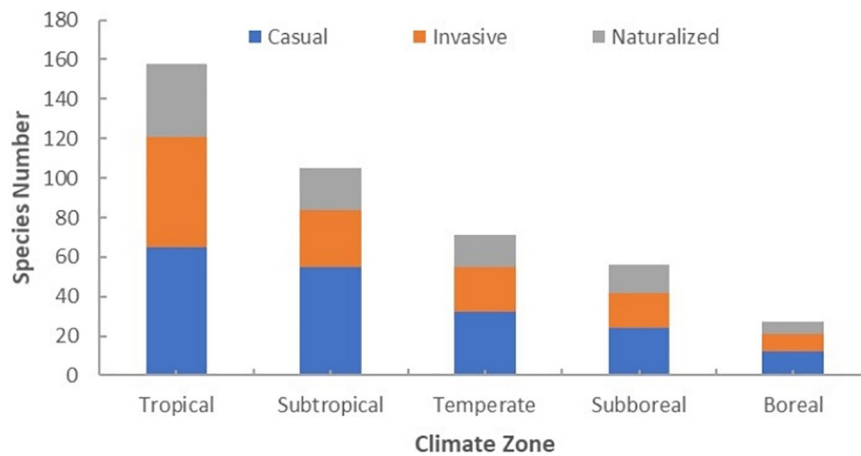


FIGURE 4 | Statistical histogram of climatic origins of non-native, casual, invasive and naturalized plant species in Hainan.

44.67% are concentrated in Fabaceae, Asteraceae and Poaceae (**Supplementary Appendix 1** “Herb_family”).

Asteraceae and Amaranthaceae also account for 30.16%, or 63 of the invasive species among 182 non-native species in total (**Supplementary Appendix 1** “Invasive_family”). For example, *Ageratum conyzoides*, *Erigeron annuus*, *Praxelis clematidea*, and *Chromolaena odorata*, are invasives within the Bawangling Nature Reserve of Changjiang where they lead to *in situ* simplification of species composition and community structure by crowding out other plants according to prior studies (Hu et al., 2011). Consistent with previous findings in other cities, invasive species of Hainan are mostly low-growing shrubs or herbs, which are known to have lower soil moisture and nutrients requirements than tree species and can often complete their life history within harsh environmental conditions (Wang et al., 2011; Pyšek et al., 2020). They also typically have very small seeds that are easily dispersed intentionally or unintentionally via human activities, such as via seed or seedling exchange among residents, transportation, or trade, as well as by natural migration along pathways of wind or water currents (Musselman, 1994; Cusack et al., 2009; Egawa, 2017; Haubrock et al., 2021).

Human socioeconomic activities can affect plant invasion processes (Wu et al., 2010; Wang et al., 2011; Zhang et al., 2015;

Egawa, 2017; Salgado et al., 2019; Zhu et al., 2019; Pyšek et al., 2020), which is consistent with our findings for Hainan. Among the 19 administrative units of the province, the administrative unit with the highest population and GDP, Haikou, had the highest PD and SR of non-native and invasive species. Moreover, the high MPD.ses and MNTD.ses values for Haikou’s invasive species (even though not significant) suggest that they are phylogenetically overdispersed, meaning that Haikou may have a high probability of being a recipient area for additional invasive species. Haikou is located at the geographic intersection of several major regional trade routes, especially the Guangdong-Hong Kong-Macao Greater Bay Area, the Beibu Gulf Economic Circle, the ASEAN Economic Circle, and the Southeast Asian Economic Circle, and these may all facilitate the arrival of invasive species in the city, such as within ships’ ballasts and on tourists (Musselman, 1994; Cuthbert and Wu, 2013). Among the 19 administrative units in Hainan Province, Haikou’s service industries and commerce are well-developed, especially tourism and transportation, compared with other administrative units in Hainan Province. This implies that ongoing development in other parts of Hainan (Central Committee of the Communist Party of China, and National Assembly of the PRC, 2020;

TABLE 2 | The numbers and percentages of non-native and invasive species found within one or more of the seven habitats.

Number of habitats	Non-native species		Casual species		Naturalized species		Invasive species	
	N	%	N	%	N	%	N	%
One	49	26.92%	24	31.58%	16	38.10%	10	15.63%
Two	59	32.42%	22	28.95%	12	28.57%	17	26.56%
Three	48	26.37%	24	31.58%	8	19.05%	18	28.13%
Four	14	7.69%	4	5.26%	5	11.90%	10	15.63%
Five	8	4.40%	1	1.32%	0	0.00%	7	10.94%
Six	3	1.65%	1	1.32%	1	2.38%	1	1.56%
Seven	1	0.55%	0	0.00%	0	0.00%	1	1.56%

N, number of species.

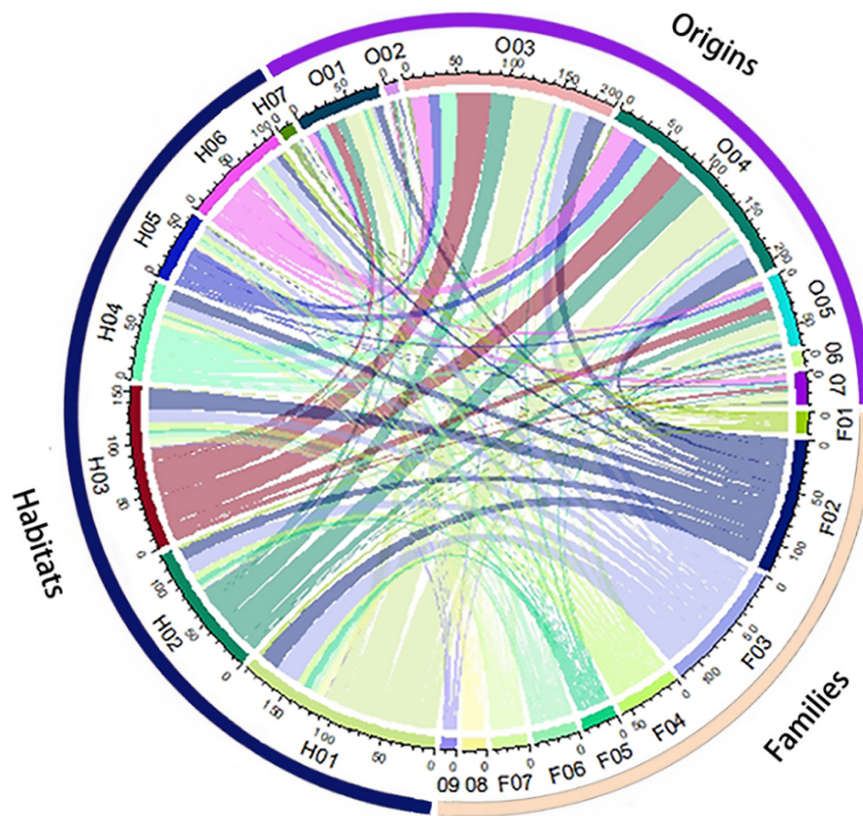


FIGURE 5 | Chord diagram denoting the relationships among the habitat, place of origin, and top nine families of non-native plants. Habitats: (H01) rural and urban built-up areas, (H02) agricultural areas, (H03) grasslands and shrublands, (H04) forest and forest margins, (H05) inland rocky outcrops, (H06) inland wetlands and water bodies, (H07) coastal areas (including mangroves, beaches, etc.); origins: (O01) Asia, (O02) Europe, (O03) North America, (O04) South America, (O05) Africa, (O06) Oceania, (O07) Unknown; top nine families: (F01) Polygonaceae, (F02) Fabaceae, (F03) Asteraceae, (F04) Poaceae, (F05) Euphorbiaceae, (F06) Amaranthaceae, (F07) Malvaceae, (F08) Verbenaceae, and (F09) Cactaceae. The arc length of each chord terminus represents the cumulative number of the habitat, place of origin, and family of non-native plants. The thickness of the chord curves represents the number of non-native plants for the habitat, place of origin, and family.

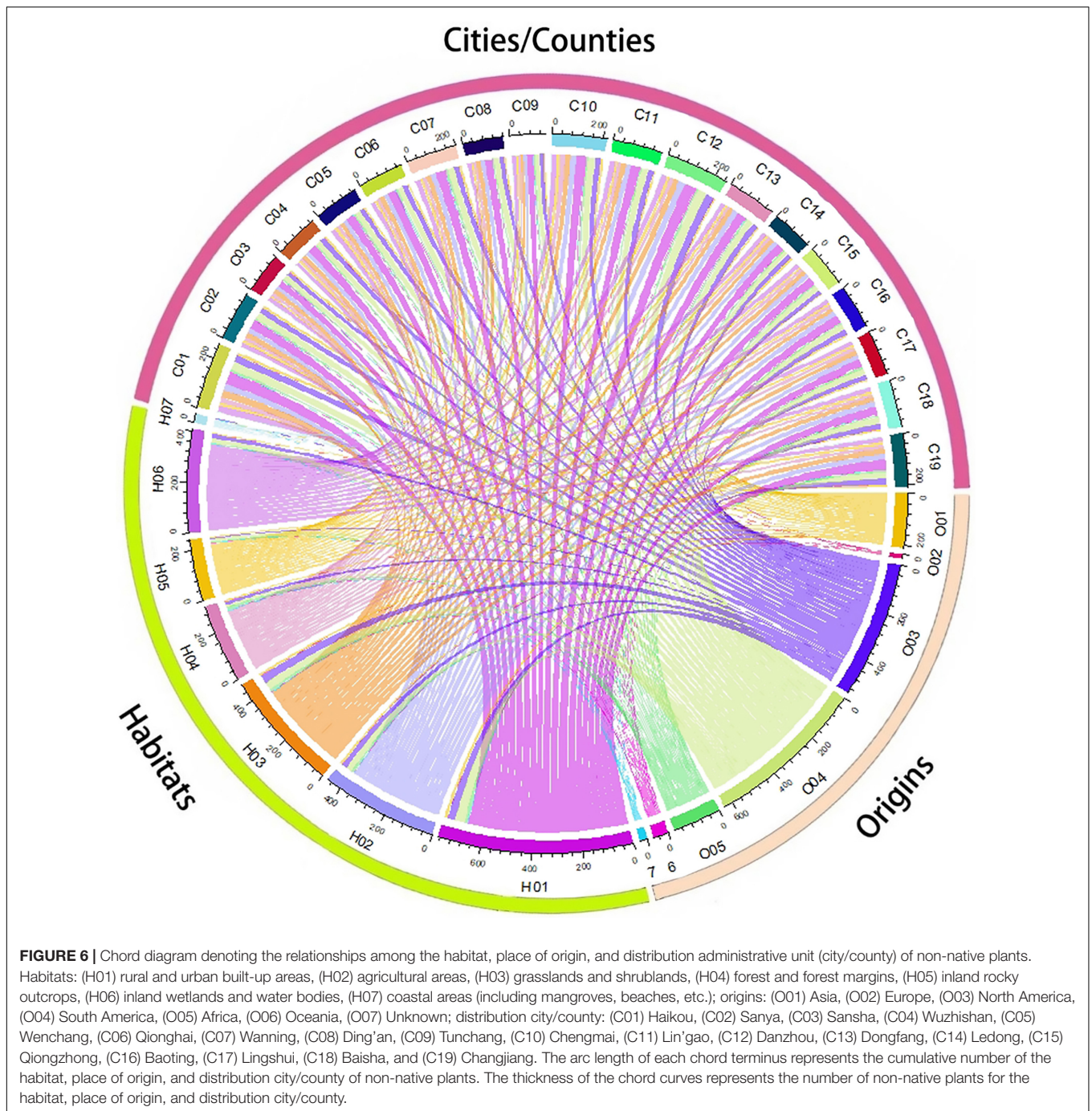
Hainan Provincial Bureau of Statistics, 2021a; NPC Standing Committee, 2021) may increase the risk of invasions if additional measures are not put in place to curtail them.

Factors Affecting Non-native Plant Species in Hainan

We found that the SR and PD of various non-native species is related to climatic factors, particularly that measures of diversity were negative correlated with the lowest temperature of the coldest month. Climatic factors are known to be related to the successful invasion of many non-native species (Zenni et al., 2014). For example, previous studies have shown that the seeds of some plants must undergo vernalization under colder temperatures before germination; this is especially true for plants from temperate regions. Therefore it is unsurprising that non-native species of Hainan originate primarily from low-latitude, warm, and humid regions of Africa, tropical Asia, tropical America and pan-tropics (Figures 4–6 and Supplementary Appendix 1). This suggests that reduction in the arrival of potentially invasive species in Hainan can be curbed

by paying particular attention to arriving ships and aircraft from these areas.

Various explanations emphasize that population density and GDP are key factors related to the composition, occurrence, and persistence of non-native species (Wu et al., 2010; Wang et al., 2011; Zhang et al., 2015; Salgado et al., 2019; Zhu et al., 2019). Generally, the higher the density of human residents, the higher the concentration of economic activities. This is consistent with our findings, in which we found that urban and rural built up areas and agricultural areas are the main habitats for invasive species. Similarly, this is in agreement with findings in prior studies showing that most invasive plants prefer to live in plant communities experiencing high levels of anthropogenic disturbance (Shan, 2003; Shan et al., 2006; Hu et al., 2011; Zhang and Xing, 2011). This may be attributed to the fact that continuous land management in these areas provides more suitable habitat for invasive species. In addition, previous studies have shown that vegetation cover and species diversity are higher in wealthy urban areas (Hope et al., 2003; Walker et al., 2009; Fan et al., 2019; Lin et al., 2021), and our study found that non-native plant diversity may also fit



this pattern. Specifically, we found that savings deposits and GDP significantly affect the distributional patterns of non-native species. This is consistent with economic development in Hainan due establishment of the Hainan Island Free Trade Port. This port and associated trade generates considerable travel and new wealth within the Haikou and Danzhou administrative units (Hainan Provincial Bureau of Statistics, 2021b; Hainan Provincial Development and Reform Commission, 2021). Thus, these units had the largest PD and, consequently, show greater evolutionary diversity and variability of non-native plants (Ricotta and Avena,

2003). They likely also have a higher risk of additional, future plant species invasions.

CONCLUSION

Our research indicates that the distributional patterns of non-native plant species in Hainan are determined by the interactions of several different factors. Specifically, we found that the diversity of non-native species is related to climatic factors, especially the highest temperature of the warmest month and the

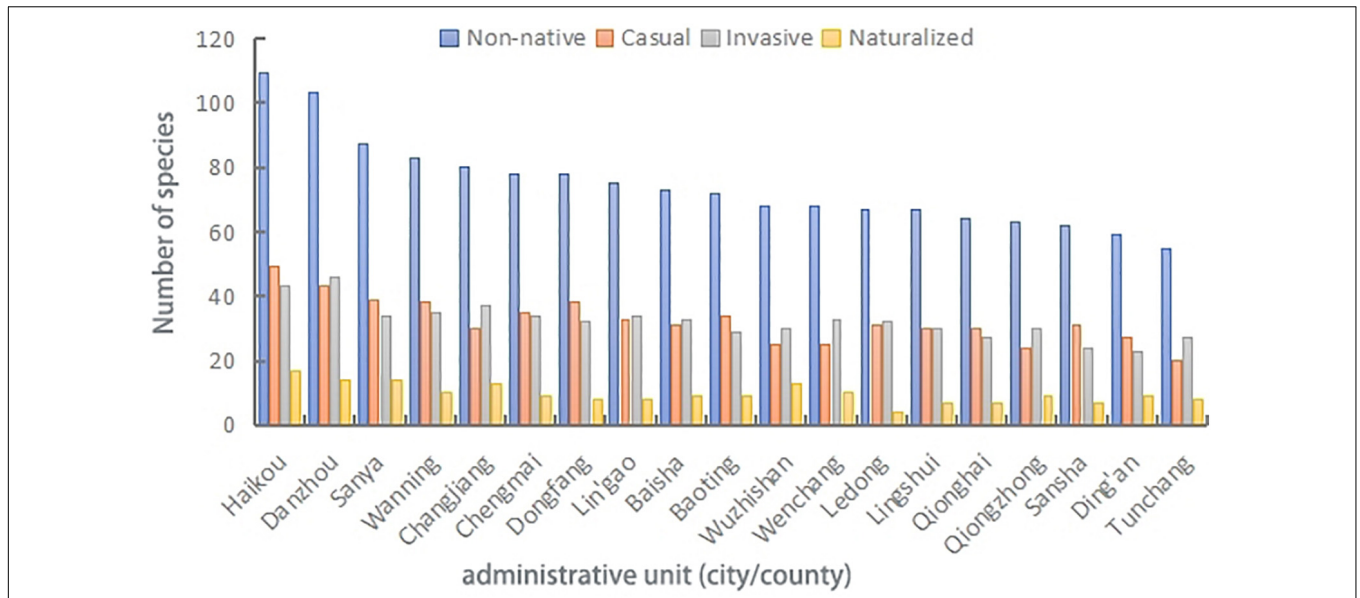


FIGURE 7 | The number of non-native, casual, invasive, and naturalized plant species in each administrative unit (city/county) within Hainan island.

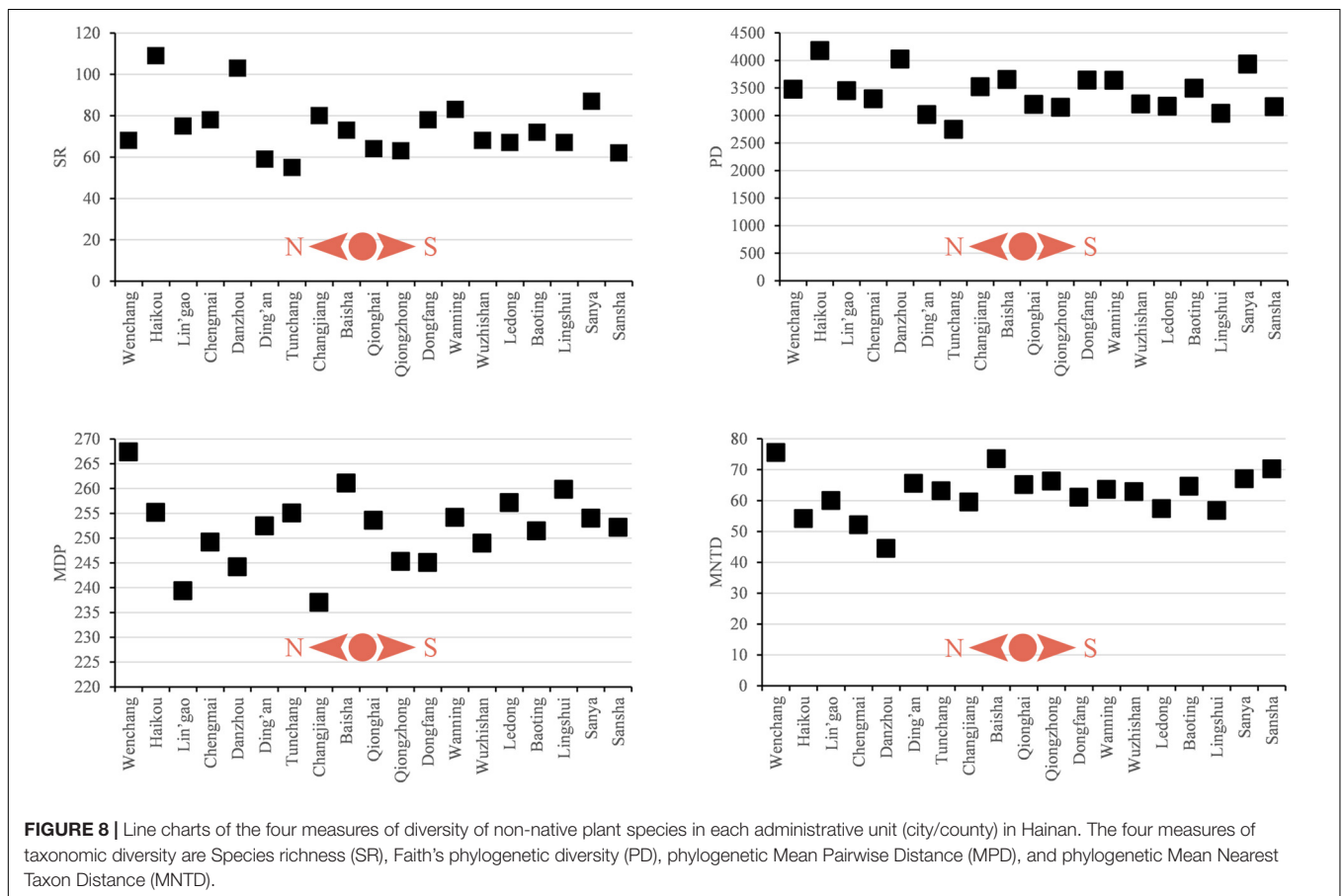


FIGURE 8 | Line charts of the four measures of diversity of non-native plant species in each administrative unit (city/county) in Hainan. The four measures of taxonomic diversity are Species richness (SR), Faith's phylogenetic diversity (PD), phylogenetic Mean Pairwise Distance (MPD), and phylogenetic Mean Nearest Taxon Distance (MNTD).

lowest temperature of the coldest month, as well as socio-economic factors, particularly GDP and tourism. The socio-economic status of the provincial capital, Haikou, appears to make it

particularly vulnerable to species invasions. As an island, Hainan is surrounded by the sea on all sides, so that its ecosystem has little communication with other regional ecosystems and is

TABLE 3 | The diversity of non-native species in each administrative unit within Hainan.

Administrative units	SR	PD	Observed MPD	MPD ses ¹	MPD <i>p</i> -value ²	Observed MNTD	MNTD ses ¹	MNTD <i>p</i> -value ²
Haikou	89	4178.08	255.19	-0.85	0.22	54.13	-0.63	0.26
Sanya	71	3930.60	254.00	-0.80	0.23	67.00	0.23	0.57
Sansha	53	3157.23	252.19	-0.80	0.23	70.21	-0.31	0.40
Wuzhishan	57	3205.49	249.00	-1.04	0.15	62.88	-0.75	0.26
Wenchang	56	3474.73	267.41	0.45	0.66	75.53	0.35	0.63
Qionghai	56	3198.62	253.60	-0.61	0.31	65.10	-0.68	0.27
Wanning	68	3637.42	254.18	-0.78	0.25	63.56	-0.23	0.41
Ding'an	51	3013.59	252.48	-0.77	0.23	65.56	-0.80	0.22
Tunchang	46	2747.51	255.05	-0.43	0.35	63.10	-1.18	0.12
Chengmai	66	3302.14	249.18	-1.14	0.13	52.14	-1.64	0.05
Lin'gao	64	3449.22	239.39	-2.09	0.01	59.96	-0.89	0.19
Danzhou	90	4021.24	244.23	-2.31	0.02	44.47	-2.02	0.03
Dongfang	67	3641.95	245.10	-1.68	0.06	61.01	-0.60	0.30
Ledong	58	3164.45	257.15	-0.43	0.36	57.34	-1.29	0.10
Qiongzong	54	3145.73	245.31	-1.37	0.09	66.26	-0.62	0.28
Baoting	61	3494.28	251.45	-0.90	0.20	64.61	-0.45	0.33
Lingshui	56	3038.00	259.83	-0.18	0.46	56.77	-1.45	0.07
Baisha	61	3653.22	261.09	-0.08	0.50	73.52	0.43	0.66
Changjiang	68	3521.34	237.05	-2.41	0.01	59.51	-0.71	0.25

¹ses, standardized effect size; ²*p*-value derived from 999 permutations to generate null models.

thus, fragile and vulnerable to invasion by foreign organisms. Therefore, the entire island may be at relatively high risk from invasion. It is critical to strengthen research on the distribution of existing invasive species, the potential hazards of established non-native species, and probable invasion mechanisms. Training garden maintenance personnel to identify invasive species and their hazards and to take preventive measures can effectively

enhance our control over their spread, while also restoring native species, reducing the introduction of non-native species, and establishing a stable ecosystem dominated by native plants. Future studies on the social and ecological complexity of Hainan and its impact on non-native plant distribution patterns can provide better strategies for preventing plant invasions and protecting native species.

TABLE 4 | The diversity of invasive species in each administrative unit within Hainan.

Administrative units	SR	PD	Observed MPD	MPD ses ¹	MPD <i>p</i> -value ²	Observed MNTD	MNTD ses ¹	MNTD <i>p</i> -value ²
Haikou	38	2543.61	235.79	1.09	0.91	97.4	1.35	0.86
Sanya	33	2284.20	236.87	0.53	0.93	97.96	1.39	0.70
Sansha	24	1713.91	237.61	-0.23	0.85	97.93	1.05	0.41
Wuzhishan	28	1883.19	232.79	-0.20	0.57	94.21	0.28	0.41
Wenchang	31	2037.73	234.37	-0.40	0.74	89.59	0.70	0.35
Qionghai	26	1758.45	235.25	-0.75	0.76	88.90	0.74	0.23
Wanning	33	2122.66	233.47	-0.28	0.69	88.98	0.51	0.39
Ding'an	23	1652.12	236.87	-0.39	0.83	96.38	0.94	0.35
Tunchang	27	1760.08	235.10	-0.64	0.77	88.48	0.73	0.27
Chengmai	33	1981.85	232.64	-1.19	0.58	79.38	0.25	0.13
Lin'gao	32	1943.36	227.95	-1.00	0.17	82.12	-0.98	0.17
Danzhou	43	2449.68	228.21	-1.14	0.10	78.33	-1.38	0.14
Dongfang	30	1913.63	230.51	-0.83	0.38	85.34	-0.22	0.21
Ledong	31	2206.20	238.97	0.36	0.98	98.08	1.81	0.64
Qiongzong	28	1836.18	234.20	-0.67	0.73	88.36	0.64	0.27
Baoting	29	1937.48	236.01	-0.42	0.82	90.83	0.93	0.33
Lingshui	30	2034.51	237.35	0.07	0.92	94.89	1.33	0.53
Baisha	31	1894.54	230.37	-0.73	0.37	85.23	-0.26	0.23
Changjiang	34	2299.95	232.55	0.50	0.60	96.59	0.29	0.68

¹ses, standardized effect size; ²*p*-value derived from 999 permutations to generate null models.

TABLE 5 | Analysis of the factors influencing plant diversity in different administrative units of Hainan.

		Non-native	Casual	Invasive	Naturalized	PD (Non-native)	MPD.ses (Non-native)	MNTD.ses (Non-native)	PD (Invasive)	MPD.ses (Invasive)	MNTD.ses (Invasive)
Socioeconomics	Population	nm	ns	ns	nm	$-1.77 \times 10^{-3*}$	$3.55 \times 10^{-6*}$	$-4.23 \times 10^{-6*}$	ns	nm	$4.36 \times 10^{-6*}$
	Total output value of Agriculture (10 thousand Yuan)	ns	nm	ns	$-1.32 \times 10^{-5*}$	nm	nm	nm	ns	nm	nm
	Total output value of Industry (10 thousand Yuan) in 2013	ns	nm	$1.03 \times 10^{-5*}$	$5.61 \times 10^{-6*}$	nm	nm	nm	ns	nm	ns
	Total retail sales of social consumer goods (10 thousand Yuan)	nm	$2.89 \times 10^{-5*}$	ns	ns	nm	$-4.71 \times 10^{-6*}$	ns	ns	nm	ns
	Number of tourists in 2013	nm	nm	nm	ns	nm	nm	nm	nm	nm	nm
	Savings deposits (10 thousand Yuan) in 2013	$-8.36 \times 10^{-6**}$	$-1.73 \times 10^{-5*}$	ns	ns	nm	$2.99 \times 10^{-6**}$	$2.54 \times 10^{-6*}$	ns	$4.23 \times 10^{-7*}$	$2.56 \times 10^{-6*}$
	GDP (0.1 billion Yuan)	$1.14 \times 10^{-1***}$	$7.49 \times 10^{-2**}$	nm	ns	2.742**	$-1.15 \times 10^{-2**}$	ns	ns	ns	$-1.16 \times 10^{-2**}$
	Area km2	ns	ns	$2.62 \times 10^{-3*}$	$-2.72 \times 10^{-1*}$	$2.43 \times 10^{-1**}$	nm	$6.48 \times 10^{-4**}$	ns	nm	ns
Biophysical Natural environment	Min temperature of coldest month (BIO6)	nm	nm	ns	ns	ns	nm	ns	nm	nm	ns
	Max temperature of warmest month (BIO5)	nm	nm	ns	ns	ns	nm	ns	ns	nm	nm
	Annual rainfall (mm)	ns	ns	ns	ns	ns	ns	nm	ns	nm	nm
	Mean temperature of warmest quarter (Bio10)	ns	nm	$-3.65*$	nm	nm	nm	$4.47 \times 10^{-1*}$	$-2.31 \times 10^{2*}$	ns	ns
	Mean temperature of coldest quarter (Bio11)	ns	2.85*	nm	nm	nm	nm	ns	ns	$2.49 \times 10^{-1*}$	$4.76 \times 10^{-1*}$
	Intercept	ns	ns	$1.63 \times 10^{2**}$	$4.01 \times 10^*$	$5.15 \times 10^{3***}$	$-3.02*$	ns	$7.52 \times 10^{3**}$	ns	ns
Adjusted R-squared	0.83	0.81	0.76	0.75	0.69	0.44	0.62	0.70	0.59	0.70	
p-value	7.77×10^{-4}	4.66×10^{-4}	1.05×10^{-2}	1.31×10^{-2}	2.53×10^{-3}	3.07×10^{-2}	3.00×10^{-2}	2.25×10^{-2}	2.78×10^{-3}	1.25×10^{-2}	
AIC	69.18	46.61	40.14	21.66	197.44	-15.06	-27.11	181.35	-28.64	-23.66	

Stepwise regression with Linear Models (LM) relate the characteristics of non-native plants in Hainan to socioeconomic variables. The minimum AIC values of the equation help determine whether to include the variable in the model, with "-" indicating exclusion from the models. Signif. codes: 0 "****" 0.001 "****" 0.01 "***" 0.05 "ns".

TABLE 6 | Analysis of influencing factors in different administrative units in Hainan.

		Non-native		Casual		Invasive (Non-native)		Naturalized (Non-native)		PD (Non-native)		MPD.ses (Invasive)		MNTD.ses (Invasive)		PD (Invasive)		MPD.ses		MNTD.ses	
		Coeff (std.Error)	r ² _{adj}	Coeff (std.Error)	r ² _{adj}	Coeff (std.Error)	r ² _{adj}	Coeff (std.Error)	r ² _{adj}	Coeff (std.Error)	r ² _{adj}	Coeff (std.Error)	r ² _{adj}	Coeff (std.Error)	r ² _{adj}	Coeff (std.Error)	r ² _{adj}	Coeff (std.Error)	r ² _{adj}	Coeff (std.Error)	r ² _{adj}
Socioeconomics	Population	3.15 × 10 ⁻⁵ (6.08 × 10 ⁻⁶)***	0.60	1.58 × 10 ⁻⁵ (3.26 × 10 ⁻⁶)***	0.57	1.11 × 10 ⁻⁵ (2.71 × 10 ⁻⁶)***	0.48	4.63 × 10 ⁻⁶ (1.92 × 10 ⁻⁶)*	0.22	6.93 × 10 ⁻⁴ (2.01 × 10 ⁻⁴)**	0.39	-1.68 × 10 ⁻⁷ (5.45 × 10 ⁻⁷)	-0.06	-3.14 × 10 ⁻⁷ (4.60 × 10 ⁻⁷)	-0.03	4.98 × 10 ⁻⁴ (1.21 × 10 ⁻⁴)***	0.49	6.05 × 10 ⁻⁷ (4.21 × 10 ⁻⁷)	0.06	8.15 × 10 ⁻⁸ (5.82 × 10 ⁻⁷)	-0.06
	Total output value of Agriculture (10 thousand Yuan)	3.05 × 10 ⁻⁵ (2.20 × 10 ⁻⁵)	0.05	2.19 × 10 ⁻⁵ (1.07 × 10 ⁻⁵)	0.16	9.66 × 10 ⁻⁶ (8.73 × 10 ⁻⁶)	0.01	-1.10 × 10 ⁻⁶ (5.23 × 10 ⁻⁶)	-0.06	7.68 × 10 ⁻⁴ (5.89 × 10 ⁻⁴)	0.04	7.12 × 10 ⁻⁷ (1.27 × 10 ⁻⁶)	-0.04	-3.61 × 10 ⁻⁷ (1.09 × 10 ⁻⁶)	-0.06	6.38 × 10 ⁻⁴ (3.77 × 10 ⁻⁴)	0.10	6.47 × 10 ⁻⁷ (1.03 × 10 ⁻⁶)	-0.04	1.38 × 10 ⁻⁶ (1.32 × 10 ⁻⁶)	0.01
	Total output value of Industry (10 thousand Yuan) in 2013	2.63 × 10 ⁻⁵ (7.60 × 10 ⁻⁶)**	0.39	1.32 × 10 ⁻⁵ (3.99 × 10 ⁻⁶)**	0.37	8.34 × 10 ⁻⁶ (3.31 × 10 ⁻⁶)*	0.24	4.83 × 10 ⁻⁶ (1.92 × 10 ⁻⁶)*	0.24	5.58 × 10 ⁻⁴ (2.29 × 10 ⁻⁴)*	0.23	-4.44 × 10 ⁻⁷ (5.41 × 10 ⁻⁷)	-0.02	-1.80 × 10 ⁻⁷ (4.69 × 10 ⁻⁷)	-0.05	3.72 × 10 ⁻⁴ (1.48 × 10 ⁻⁴)*	0.24	6.85 × 10 ⁻⁷ (4.18 × 10 ⁻⁷)	0.09	2.14 × 10 ⁻⁷ (5.85 × 10 ⁻⁷)	-0.05
	Total retail sales of social consumer goods (10 thousand Yuan)	8.52 × 10 ⁻⁶ (2.28 × 10 ⁻⁶)**	0.43	4.22 × 10 ⁻⁶ (1.21 × 10 ⁻⁶)**	0.40	2.52 × 10 ⁻⁶ (1.04 × 10 ⁻⁶)*	0.23	1.77 × 10 ⁻⁶ (5.44 × 10 ⁻⁷)**	0.36	1.99 × 10 ⁻⁴ (6.64 × 10 ⁻⁵)**	0.32	3.85 × 10 ⁻⁸ (1.71 × 10 ⁻⁷)	-0.06	5.91 × 10 ⁻⁸ (1.45 × 10 ⁻⁷)	-0.05	1.31 × 10 ⁻⁴ (4.32 × 10 ⁻⁵)**	0.33	3.33 × 10 ⁻⁷ (1.13 × 10 ⁻⁷)**	0.31	2.04 × 10 ⁻⁷ (1.75 × 10 ⁻⁷)	0.02
	Number of tourists in 2013	2.39 × 10 ⁻⁶ (8.04 × 10 ⁻⁷)**	0.32	1.25 × 10 ⁻⁶ (4.11 × 10 ⁻⁷)**	0.33	5.85 × 10 ⁻⁷ (3.62 × 10 ⁻⁷)	0.09	5.59 × 10 ⁻⁷ (1.77 × 10 ⁻⁷)**	0.35	6.54 × 10 ⁻⁵ (2.11 × 10 ⁻⁵)**	0.34	2.63 × 10 ⁻⁸ (5.46 × 10 ⁻⁸)	-0.05	6.06 × 10 ⁻⁸ (4.44 × 10 ⁻⁸)	0.05	3.96 × 10 ⁻⁵ (1.44 × 10 ⁻⁵)*	0.28	1.13 × 10 ⁻⁷ (3.50 × 10 ⁻⁸)**	0.36	9.14 × 10 ⁻⁸ (5.39 × 10 ⁻⁸)	0.10
	Savings deposits (10 thousand Yuan) in 2013	3.92 × 10 ⁻⁶ (1.06 × 10 ⁻⁶)**	0.43	1.94 × 10 ⁻⁶ (5.61 × 10 ⁻⁷)**	0.39	1.15 × 10 ⁻⁶ (4.82 × 10 ⁻⁷)*	0.22	8.26 × 10 ⁻⁷ (2.50 × 10 ⁻⁷)**	0.37	9.31 × 10 ⁻⁵ (3.05 × 10 ⁻⁵)**	0.33	2.48 × 10 ⁻⁸ (7.88 × 10 ⁻⁸)	-0.06	3.36 × 10 ⁻⁸ (6.70 × 10 ⁻⁸)	-0.05	6.17 × 10 ⁻⁵ (1.98 × 10 ⁻⁵)**	0.34	1.60 × 10 ⁻⁷ (5.09 × 10 ⁻⁸)**	0.34	1.05 × 10 ⁻⁷ (8.00 × 10 ⁻⁸)	0.04
	GDP (0.1 billion Yuan)	4.25 × 10 ⁻² (7.66 × 10 ⁻³)***	0.64	2.09 × 10 ⁻² (4.25 × 10 ⁻³)***	0.58	1.36 × 10 ⁻² (3.79 × 10 ⁻³)**	0.41	7.93 × 10 ⁻³ (2.18 × 10 ⁻³)**	0.42	9.74 × 10 ⁻¹ (2.50 × 10 ⁻¹)**	0.45	-2.19 × 10 ⁻⁴ (7.17 × 10 ⁻⁴)	-0.06	-1.18 × 10 ⁻⁴ (6.13 × 10 ⁻⁴)	-0.06	6.50 × 10 ⁻¹ (1.60 × 10 ⁻¹)***	0.48	1.13 × 10 ⁻³ (5.17 × 10 ⁻⁴)*	0.18	3.99 × 10 ⁻⁴ (7.59 × 10 ⁻⁴)	-0.04
	Biophysical	Area km2	7.03 × 10 ⁻³ (3.54 × 10 ⁻³)	0.15	3.41 × 10 ⁻³ (1.85 × 10 ⁻³)	0.12	3.22 × 10 ⁻³ (1.31 × 10 ⁻³)*	0.23	4.03 × 10 ⁻⁴ (8.84 × 10 ⁻⁴)	-0.05	1.88 × 10 ⁻¹ (9.43 × 10 ⁻²)	0.15	-5.86 × 10 ⁻⁵ (2.17 × 10 ⁻⁴)	-0.06	3.44 × 10 ⁻⁵ (1.85 × 10 ⁻⁴)	-0.06	1.19 × 10 ⁻¹ (6.21 × 10 ⁻²)	0.14	-4.43 × 10 ⁻⁵ (1.77 × 10 ⁻⁴)	-0.06	-1.51 × 10 ⁻⁴ (2.28 × 10 ⁻⁴)
Natural environment	Min temperature of coldest month (Bio6)	-1.34 (4.33 × 10 ⁻¹)**	0.34	-6.47 × 10 ⁻¹ (2.31 × 10 ⁻¹)*	0.29	-4.51 × 10 ⁻¹ (1.81 × 10 ⁻¹)*	0.23	-2.44 × 10 ⁻¹ (1.07 × 10 ⁻¹)*	0.20	-3.91 × 10 (1.08 × 10)**	0.41	1.54 × 10 ⁻² (2.98 × 10 ⁻²)	-0.05	-1.11 × 10 ⁻² (2.55 × 10 ⁻²)	-0.05	-1.90 × 10 (8.28)*	0.20	-1.29 × 10 ⁻² (2.44 × 10 ⁻²)	-0.04	1.70 × 10 ⁻² (3.17 × 10 ⁻²)	-0.04
	Max temperature of warmest month (Bio5)	6.07 × 10 ⁻¹ (9.13 × 10 ⁻¹)	-0.03	2.19 × 10 ⁻¹ (4.734 × 10 ⁻¹)	-0.05	1.06 × 10 ⁻¹ (3.59 × 10 ⁻¹)	-0.06	2.82 × 10 ⁻¹ (1.96 × 10 ⁻¹)	0.06	2.56 × 10 (2.38 × 10)	0.01	1.69 × 10 ⁻² (5.06 × 10 ⁻²)	-0.06	6.74 × 10 ⁻² (4.00 × 10 ⁻²)	0.10	8.54 (1.60 × 10)	-0.04	6.39 × 10 ⁻² (3.84 × 10 ⁻²)	0.09	6.16 × 10 ⁻² (5.19 × 10 ⁻²)	0.02
	Annual rainfall (mm)	-1.07 × 10 ⁻² (8.70 × 10 ⁻³)	0.03	-7.08 × 10 ⁻³ (4.34 × 10 ⁻³)	0.09	-4.07 × 10 ⁻³ (3.39 × 10 ⁻³)	0.03	4.64 × 10 ⁻⁴ (2.04 × 10 ⁻³)	-0.06	-3.83 × 10 ⁻¹ (2.26 × 10 ⁻¹)	0.10	4.75 × 10 ⁻⁴ (4.85 × 10 ⁻⁴)	0.00	-1.77 × 10 ⁻⁴ (4.24 × 10 ⁻⁴)	-0.05	-1.89 × 10 ⁻¹ (1.51 × 10 ⁻¹)	0.03	-8.99 × 10 ⁻⁵ (4.08 × 10 ⁻⁴)	-0.06	2.14 × 10 ⁻⁴ (5.29 × 10 ⁻⁴)	-0.05
	Mean temperature of warmest quarter (Bio10)	5.52 (4.01)	0.05	4.35 (1.90)*	0.20	1.29 (1.62)	-0.02	-1.14 × 10 ⁻¹ (9.55 × 10 ⁻¹)	-0.06	1.48 × 10 ² (1.09 × 10 ²)	0.05	-1.30 × 10 ⁻¹ (2.31 × 10 ⁻¹)	-0.04	-1.58 × 10 ⁻² (1.99 × 10 ⁻¹)	-0.06	4.92 × 10 (7.29 × 10)	-0.03	-7.95 × 10 ⁻² (1.90 × 10 ⁻¹)	-0.05	-7.43 × 10 ⁻² (2.47 × 10 ⁻¹)	-0.06
	Mean temperature of coldest quarter (Bio11)	1.19 (3.67)	-0.06	2.25 (1.81)	0.03	-5.62 × 10 ⁻¹ (1.42)	-0.05	-4.97 × 10 ⁻¹ (8.18 × 10 ⁻¹)	-0.04	6.76 × 10 (9.65 × 10)	-0.03	1.42 × 10 ⁻¹ (1.97 × 10 ⁻¹)	-0.03	1.52 × 10 ⁻¹ (1.68 × 10 ⁻¹)	-0.01	3.88 × 10 (6.33 × 10)	-0.04	1.65 × 10 ⁻¹ (1.60 × 10 ⁻¹)	0.00	3.71 × 10 ⁻¹ (1.94 × 10 ⁻¹)	0.14

A linear model (LM) was used for single-factor regressions to link the characteristics of exotic plants in Hainan Province with socio-economic variables. Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

L-YG: writing—original draft, data curation, formal analysis, investigation, and visualization. MN: methodology and data curation. AH: validation and writing—review and editing. Q-WL: conceptualization. KB: writing—review. L-JD: data collection and funding. SQ: data collection and curation. H-FW: conceptualization, supervision, project administration, and funding acquisition. All authors contributed to the article and approved the submitted version.

FUNDING

This study was funded by the National Natural Science Foundation of China (32160273) and Shanghai Key

Lab for Urban Ecological Processes and Eco-Restoration (SHUES2020A07) both to H-FW.

ACKNOWLEDGMENTS

We thank the editor and two reviewers for valuable comments that improved the quality of the manuscript.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2022.838591/full#supplementary-material>

Supplementary Appendix 1 | List of non-native plants and statistical tables in Hainan Province, China.

Supplementary Appendix 2 | Socioeconomic and environmental variables for each administrative unit.

Supplementary Appendix 3 | Coordinates from the field survey sampling locations.

Supplementary Appendix 4 | Figure of the curvilinear relationship between land area and non-native species diversity.

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