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探討臺灣外來植物豐富度沿海拔變化的模式：物種溫度偏好或人類活動強度的影響？

Is decreasing richness of alien plant species along elevation in Taiwan caused by species temperature preference or intensity of human activities?

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Abstract

Alien are those species that were brought from their native ranges to the introduced ranges by humans. Studies around the world described decreasing species richness-elevation patterns of alien plants. However, the mechanisms behind these patterns remain unclear. Hence, we proposed two hypotheses to explain this pattern. The first is the species preference temperature hypothesis, stating that alien species richness results from the size of the species pool determined by temperature preferences of these species in their native range. The second is the human activity hypothesis, assuming that the intensity of human activities, serving as the source of propagule pressure and disturbance, is positively related to alien species richness. We used the survey data from the Survey of Invasive Alien Plants in Taiwan (led by Dr. Shan-Hua Wu) to describe the species richness-elevation pattern in Taiwan, to quantify the relative importance of these two hypotheses, and to further find evidence for both hypotheses.

For describing the alien species richness-elevation pattern in Taiwan, we used existing systematical sampling survey data and standardized sampling effort in each 1 km × 1 km cell by plot-based rarefaction. We confined the analysis to two habitat types, roadside and agricultural land, which have enough sample size and are distributed widely along the elevation gradient. For quantifying the relative importance of these two hypotheses, we used potential species pool size and the proportion of land-use in the surrounding area of cells to represent species temperature preference hypothesis and human activity hypothesis, respectively. Multiple linear regression with variation partitioning was performed on standardized species richness with explanatory variables which represent two hypotheses. In species-level analysis, we compared the preference temperature of individual species between Taiwan and their native ranges. We regressed temperature deviation between Taiwan and their native ranges on several species attributes, such as bioclimatic origin and economic usage, to identify a possible reason for the larger temperature deviation of some species.

The results showed that the alien species richness-elevation pattern is monotonically decreasing in Taiwan. The species temperature preference hypothesis explained more variation in alien species richness than the human activity hypothesis. Species-level analyses showed that species preference temperatures in the native range and Taiwan are well correlated (*r* = 0.67), and species preference temperatures in Taiwan match their native range in the case of 257 out of 396 species. However, temperate-origin and non-ornamental alien species in Taiwan tend to occur in habitats warmer than in their native ranges. The elevation distribution of alien species in Taiwan is from lowland to certain elevations. Many alien species occurring in higher elevations are temperature generalists, adapting to both lower and higher temperatures, and most of them are of temperate origin. We conclude that alien species mainly spread from the lowland and are gradually being filtered out along the elevation gradient based on their native temperature preference (bioclimatic origin), resulting in the decreasing alien species richness-elevation pattern in Taiwan.

Keywords: agriculture, alien plant species, bioclimatic origin, human activity, introduced range, land-use, native range, roadside, species richness-elevation pattern, species temperature preference, Survey of Invasive Alien Plants in Taiwan, variation partitioning

中文摘要

外來種指的是由人類帶入原生地以外地區的物種。世界各地的研究大多指出外來植物物種豐富度沿海拔上升而下降，然而其背後機制尚未明瞭，因此我們提出兩個假說來解釋這個模式，其一為物種溫度偏好假說，外來種物種豐富度與其在引入地的外來種物種庫大小相關，而外來種物種在其原生地的溫度偏好決定引入地的物種庫大小。另一為人類活動假說，我們假設外來種物種豐富度與人類活動的強度成正比，因為人類活動產生的拓殖體壓力以及干擾有助於外來種成功入侵引入地。我們使用全國外來入侵植物調查的樣區資料檢視外來植物物種豐富度沿海拔變化模式，並量化比較兩個假說對這個模式的貢獻，為物種溫度偏好假說提供更多的證據支持。

我們以現有的系統性調查樣區資料，使用標準化樣格內努力量的物種豐富度繪製臺灣外來植物物種豐富度沿海拔變化模式。為確保不同海拔梯度有足夠的樣本數分布，我們分析的範圍限制在路邊和農業用地這兩種棲地。使用潛在物種庫和樣格周邊的土地利用比例分別代表物種偏好假說與人為活動假說，對標準化物種豐富度進行多重線性迴歸和變異分配，比較兩假說的貢獻。在物種層級的分析中，我們比較每種外來植物其在原生地和臺灣的偏好溫度，將兩地之溫度差與物種特質(例:生物氣候起源、經濟用途)做迴歸分析，尋找在原生地及引入地較大溫度差的物種擁有的特質。

結果發現臺灣的外來植物物種豐富度沿海拔是單調遞減的模式。相較於人類活動假說，物種溫度偏好假說對此模式解釋較多的變量。外來種在其原生地與臺灣的物種偏好溫度成高度相關($r = 0.67$)，本研究的 396 種植物中，有 257 種在兩地的溫度偏好相符。來自於溫帶和非園藝用途的外來種在臺灣傾向生長較原生地溫暖的地方。外來種在臺灣的分布上，大多是由低海拔地區至某個海拔，而分布在海拔較高的大都是溫度上的廣適應物種，可以在高或低溫生活，並來自溫帶地區。這些證據顯示臺灣的外來種物種豐富度沿海拔模式受物種原生地的溫度偏好影響。外來種由低海拔向上擴散，並逐漸根據外來種原生地的溫度偏好一一被溫度梯度過濾，導致單調遞減的外來種物種豐富度沿海拔變化模式。

關鍵字：農業活動、外來植物、生物氣候起源、人為活動、引入地、原生地、土地利用、路邊、物種豐富度海拔模式、物種溫度偏好、外來入侵植物全國現狀調查、變異分配

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Introduction

Species richness-elevation pattern describes the change of species richness along the elevation gradient. This pattern was intensively studied because the elevation gradient is related to several abiotic factors, such as temperature, precipitation, and solar radiation, which change sharply within a short distance (Körner 2007). Elevation gradient is a natural experimental design to study the community response to environmental gradients. Studies done in different regions on different taxa showed that there are various shapes of species richness-elevation patterns, which can be classified into four types: decreasing, low plateau, low plateau with a mid-elevational peak, and mid-elevation peak (unimodal) (McCain & Grytnes 2010). In the case of plant species, most studies focusing on native species (i.e., species that evolved in the studied region or naturally immigrated there) show that the unimodal pattern dominates the species richness-elevation pattern around the world (Rahbek 2005). In contrast, studies focusing on alien species that has been accidentally or intentionally introduced to the region by human migration and transportation across geographic boundaries (Richardson et al. 2000b), found that the species richness-elevation pattern is usually monotonically decreasing as the elevation rises (Guo et al. 2018). The difference in the shapes of native and alien species richness-elevation patterns may be caused by different mechanisms that determine these patterns.

The native species richness-elevation patterns are mainly shaped by climatic factors (Kluge et al. 2006, Kessler et al. 2011), spatial factors (Rosenzweig 1995, Romdal and Grytnes 2007), biotic factors, and evolutionary history (i.e., processes related to speciation, e.g., presence of geographical barriers) (Kessler et al. 2016). In contrast to native species, the alien species richness-elevation patterns not only develop by the same set of factors as native species except for evolutionary history, but also by the anthropogenic factors. Alien species adapted to the environment of their native habitats. They came from various types of habitats, where alien

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species adapt. One of the examples is temperature preference of each alien species in their native ranges. The relative proportion of alien species in the alien flora in the introduced ranges with warm and cold temperature preferences may determine the shape of alien species richness-elevation pattern. If more cold-adapted species are present in the introduced range, the higher will the peak of alien species richness-elevation pattern be. In addition, dispersal of alien species heavily relies on human activities, so the anthropogenic factors also contribute to the alien species richness-elevation patterns. Unlike native plants, which have been established in a given region for a long time to be able to adapt to the environment, alien plants arrived relatively recently, so they had a much shorter time to adapt to the local environment and must be affected by the abiotic and biotic factors. As a result, the alien species richness-elevation pattern probably reflects more the recent immigration of aliens to the region, and the relative importance of evolutionary history to alien species richness-elevation patterns might be quite small.

According to the Richardson et al. (2000b), invasion process of alien species can be divided into three stages: introduction, naturalization and invasion. For each stage, there are different barriers that prevent alien species from moving to the next stage. In the introduction stage, alien species cross the geographic barrier to the introduced regions and survive in the local environment, but they cannot maintain a sustainable population by themselves; species in this stage are called casual species. In the naturalization stage, alien species overcome the reproductive barrier and establish a stable population without human’s aids; these species are called as naturalized species. In the invasion stage, alien species can disperse to habitats far from their parent individuals. They can establish in the human disturbed habitats and undisturbed habitats, overcoming the environmental barriers and the competition with local biota; such species are called invasive species.

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The shape of alien species richness-elevation pattern is closely related to the invasion success of alien species, i.e., the successful introduction, naturalization and dispersal of alien species (O'Loughlin and Green 2017). Invasion success of alien species depends on three aspects: habitat invasibility, species invasiveness, and propagule pressure (Lonsdale 1999). Habitat invasibility indicates how the recipient habitats are prone to be invaded, considering the habitats' resident species and environment (Williamson 1996). It can be attributed to two groups of factors, one related to the actual amount of available resources, and the other related to biotic interactions among resident species. Davis et al. (2000) proposed the theory of fluctuating resource availability, which pointed out that alien species can invade only habitats that provide resources unused by resident species. Availability of nutrients is increased by the environmental processes that add additional nutrients to the habitat (e.g., eutrophication by adding fertilizer) or by the removal of the resident species that are currently using the resources (e.g., by disturbance) (Davis et al. 2000). The amount of available resources for alien species is also influenced by the intrinsic characteristics and life history of native species, namely their functional diversity, resource usage efficiency and reproductive ability (Levine, Adler & Yelenik 2004). The higher the difference between the number of resources being used by native species and the total amount of resources available, the higher is the invasibility of the habitat. In addition, habitat invasibility is also determined by the biotic interactions among resident species (e.g., mutualists and predators) with positive or negative impacts. Non-specific mutualists enhance the competitiveness of alien species and thus increase the invasibility of the recipient habitats (Richardson et al. 2000a). On the other hand, non-specific pathogens and predators attack the alien species, in turn, serve as resistances of community against alien species invasion (D'Antonio 1993; Levine, Adler & Yelenik 2004).

The biological attributes of alien species related to their ability to invade habitats are called species invasiveness (Williamson 1996). Species with traits that facilitate resource

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uptake, reproduction, dispersal, and adaptation of new environments have stronger species invasiveness (Pyšek & Richardson 2008). For example, the bioclimatic origin of alien species usually means that species can adapt to the climates similar to their native ranges. When the alien species reach the introduced ranges with climates similar to their native ranges, their chance of successful establishment increases (Hayes and Barry 2008; Richardson and Pyšek 2012).

Another prerequisite for invasion success is propagule pressure, a measure of number of individuals per release event and number of discrete release events (Lockwood et al. 2005). Propagule can be any kind of tissue that can develop into an individual, e.g., seeds, vegetative shoots and the whole plant. A release event refers to any event that distributes propagules to a new environment, e.g., plants release their seeds to the neighborhood, or human transport the soil which includes some bulbs of alien species to a new field. Habitats with higher propagule pressure receive propagules frequently or receive more propagule in one release event. Lockwood et al. (2005) hypothesized that higher propagule pressure allows alien species to conquer environmental stochasticity and the Allee effect more easily when they are newly introduced. Reduced population size may lead to unsuccessful pollination resulting in mate limitation. The more individuals were released can let alien species avoid extinction due to the small population size. Also, the fluctuating environmental conditions (e.g., winter or drought period) sometimes cause unsuccessful invasions. The failure can be reduced by the repeated introduction which helps alien species to pass the unfavorable time and encounter suitable timing to invade successfully (Lockwood et al. 2005). An increasing number of release events enhances the probability of invasion success (Lockwood et al. 2005). Then, increased propagule pressure may result in promoting genetic variation in the recently introduced populations, and enhance the ability of alien species to overcome the new selection pressures in the introduced ranges (Ahlroth et al. 2003).

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Becker et al. (2005) proposed two contrasting hypotheses for explaining the decreasing alien species richness-elevation pattern: poor adaptation of alien species to colder conditions at higher elevations, and low propagule pressure at higher elevations. Built on Becker's study, we introduced two testable hypotheses for explaining the possible mechanisms responsible for the alien species richness-elevation pattern, namely *species temperature preference hypothesis* and *human activity hypothesis*. In this study, we further confined the conditions of poor adaptation at higher elevations to temperature, which is one of the primary factors that determine plant growth (Went 1953; Thakur et al. 2010). The climatic barriers to alien species invasion related to temperature include the length of the growing season and the duration of frost. In *species temperature preference hypothesis*, we assume that the species richness of alien species in given region results from the size of the species pool, and this in turn is determined by the species temperature preferences of these species in their native range. The alien species' naturalization success is associated with close climate matching between their native ranges and introduced ranges (Thuiller et al. 2005; Essl et al. 2011). The temperature of the introduction ranges acts as a selection filter; only the alien species which have temperature preferences matching the temperature of introduced ranges can potentially contribute to the species pool of the introduced ranges.

On the contrary, *human activity hypothesis* states that the higher alien species richness will be in regions with higher propagule pressure and disturbance related to human activity. Both propagule pressure and availability of unoccupied habitats with available extra resources are also important for the spread of alien species. Anthropogenic land-use, such as agriculture, provides the conditions of increasing propagule pressure of alien species and high unused resource availability by resident plants. For example, agriculture activities remove the native plant covers in the field (disturbances and removal of original competitors) and add fertilizer into the soil (providing extra unused nutrients). After those alien species establish, they produce

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propagule pressure to the surroundings and promote the expansion of the distribution of alien species. The crop seeds used for agriculture are often accidentally mixed with alien seeds (Mack 2004), giving the alien species' propagules access to farmland. Transportation land-use like roadside is also affected by human disturbances and serves as the corridor for the dispersal of alien plants (Spellerberg 1998; Parendes and Jones 2000). Farmlands and roadsides, therefore, serve as the main alien species reservoirs producing propagules to spread to neighboring regions. Most human populations reside in lower elevations and thus the propagule pressure decreases along the elevation gradient.

Even if we assume these two hypotheses can explain the alien plant species richness-elevation patterns, it is difficult to differentiate which is the main cause of this pattern because along the elevation gradients, since the temperature and human activity gradients are highly correlated along the elevation gradients (Pauchard and Alaback 2004). In Taiwan, there are several studies about alien plant species, but most of them are confined to regional floristic investigations (Wu 2006; Liu 2011; Lu 2021) and evaluation of invasiveness (Chang 2007). One study described the decreasing alien species richness-elevation relationship, but did not unveil the possible mechanisms of the pattern (Sun 2009).

In this study, we chose Taiwan as the study region because as a mountainous island with an elevation reaching 3952 m a.s.l., it provides a wide elevation gradient for testing the species temperature preference hypothesis. Also, as in other places of the world, most of the human population in Taiwan resides in the lower elevation regions, allowing us to test the human activity hypothesis. We used the Survey of Invasive Alien Plants in Taiwan dataset, collected by Dr. Shan-Hua Wu and colleagues between 2009-2012 (Wu 2012), which includes systematically surveyed plots covering the whole Taiwan island on arbitrarily defined habitat types with frequent occurrence of alien species. This unique dataset offers a representative source to describe the alien species richness-elevation pattern. We aim to (1) describe the alien species richness-elevation pattern of alien plants in Taiwan, (2) quantify the contribution of the species temperature preference hypothesis and human activity hypothesis to the elevational species richness pattern of alien plants in Taiwan, and (3) further elaborate on possible explanations related to both hypotheses.

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Materials and Methods

Study area and sampling design

Taiwan is a mountainous island located in the Western Pacific Rim surrounded by China, Japan, and the Philippines. The shape of the island is long and narrow, ranging from 21°55’ to 25°20’N, 119°30’ to 122°00’E. The mountains in Taiwan reach up to 3,952 m a.s.l. and the mountainous area accounts for two-thirds of the area of the island, most of which are in the center of the island in a north-south direction, forming the Central Mountain Range. The Tropic of Cancer crosses through the center of Taiwan, causing the north to have a subtropical climate and the south to have a tropical climate. The mean annual temperature in lowlands ranges between 22°C in northern part (Keelung) and 25°C in the southern part (Hengchun); in the middle elevation the mean annual temperature is around 10°C (Alishan, 2406 m a.s.l.) and in highest elevation it reaches as low as 3.7°C (Yushan, station near 3950 m a.s.l.) (Huang & Hsieh 1994). The mean annual precipitation in the lowlands ranges between 3445 mm in the northeast, affected by winter monsoon (Keelung) and without a dry season, to as low as 1700 mm in southwest, with a dry season in winter and a wet season in summer and autumn because of the southeast summer monsoon. In summer and autumn, typhoons strike with strong winds and heavy rains. Rapid elevation change combined with subtropical climate creates diverse habitats resulting in high plant diversity, with more than 4,200 vascular plant species in 35,800 km^2 (Hsieh 2002). In Taiwan, the most intensive human development occurs on the western lowland plains, while the lowest population density occurs in the eastern longitudinal valley; mountain regions are practically not inhabitat. From the latest naturalized species list (Chang-Yang et al. 2022), there are 695 species from 400 genera and 95 families that are naturalized in Taiwan, with the most dominant family being Poaceae (97 species), followed by Asteraceae (93 species), and Fabaceae (79 species).

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The survey data were derived from the database of the Survey of Invasive Alien Plants in Taiwan (Wu 2012). The survey, organized by Dr. Wu, Shan-Hua and conducted by seven field survey groups between the years 2009 to 2012, covers the Taiwan island and surrounding outlying islands of Taiwan as the study area. The authors divided the study area into 1 km × 1 km cells and they systematically chose 1225 cells, covering 3% area of the Taiwan (Fig. 1). Surveyed habitat were arbitrarily classified into 20 types in this database. In each cell, available habitat types were distinguished, and each sampled by five 1 m × 10 m plots (fewer than five plots were sampled in smaller habitats). We only selected cells on the Taiwan island to simplify the complexity of possible mechanisms that affect the alien species richness-elevation pattern (i.e. not considering cells surveyed in outlying islands). To confirm the alien species richness-elevation pattern, for further analysis we chose only four habitat types (agricultural land, orchard, abandoned agricultural land, and roadside) which are distributed widely along the elevation gradient. We merged agricultural land, orchard, and abandoned agricultural land into one habitat type named agriculture habitat because they imply similar land-use management to ensure a large enough sample size. Overall, the survey recorded 562 alien plant species across all habitat types. After filtering and merging the data, we included in our analysis 881 cells containing 333 alien species in the roadside habitat, and 576 cells containing 315 species in the agriculture habitat. In total, 901 cells containing 376 alien plant species were selected for further analysis. In our analysis, the nomenclature of species followed the Catalogue of life in Taiwan (TaiCoL, https://taibnet.sinica.edu.tw/).

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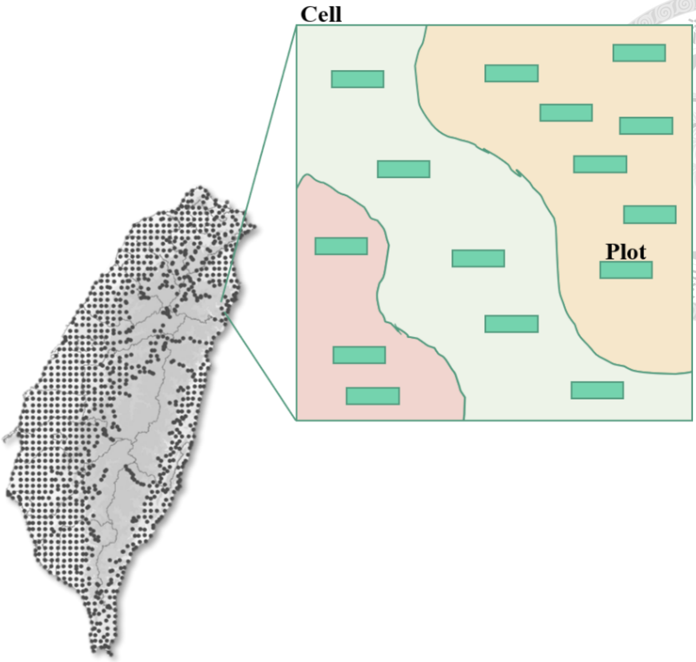

Figure 1. Sampling design of Survey of Invasive Alien Plants in Taiwan. The black dots are cells that were sampled throughout Taiwan island. The colors in the cell refer to different habitat types. For each habitat type, there are five plots which were surveyed.

Alien species occurrences

We included all the alien species in the Taiwan mainland in the Survey of Invasive Alien Plants in Taiwan from all the habitat types because we want to explore whether there is a consistent trend that these alien species preserve their native temperature preference in Taiwan. The species we used are listed in the Appendix 2.

For the alien species in their native range, we first downloaded species occurrences on Global Biodiversity Information Facility (GBIF) (GBIF.org 2022) by the function *occ_data* from the R package *rgbif* (Chamberlain et al. 2022), or manually from its website for the species with more than 100,000 occurrences. We also retrieved the species' native range information on Plants of the World Online (POWO) (POWO 2022). We looked up the species codes in the

POWO for the species in our alien species list, and we accessed the POWO native ranges information by passing species codes to the web crawler to scrape the texts of native ranges of each species (by functions from the R package *rvest*). We selected the native species occurrences by the native range polygons, which were created by using the text of native ranges to select the geographic region on the map. The map was provided by Biodiversity Information Standards (Brummitt 2001). For the alien species occurrences in Taiwan, we downloaded them from four sources, namely GBIF, Survey of Invasive Alien Plants in Taiwan, National Vegetation Database of Taiwan (Chiou et al. 2009), and herbarium records (TAI, TAIF, HAST, and TNM, compiled by Huan-Yu Lin from data provided by Chang-Fu Hsieh, Chien-Wen Chen, Chien-Fan Chen, Ching-I Peng, Kuo-Fang Chung, and Chun-Lin Huang). We used the same method to extract data from GBIF. In the Survey of Invasive Alien Plants in Taiwan, we took the coordinates of the centroid of the 1 × 1 km cell as the coordinates for those species in that cell. The National Vegetation Database of Taiwan provides species composition data and coordinates of the forest plots. We selected species within our alien species list and used the coordinates of the forest plots as the alien species occurrences. We also used the herbarium database to provide species occurrences for alien species.

Environmental factors and species attributes

To extract the information about the environment and landscape context to use as explanatory variables for alien species richness, we used the centroids of the plots in each cell as the coordinate of each cell. Two sets of variables, potential species pool size and land-use, were derived as proxies for the two hypotheses we tested in this study.

For species temperature preference hypothesis, we use the *potential species pool size,* the number of alien species whose optimal temperature range overlaps with the mean annual temperature of each cell, to represent the number of alien species that could potentially establish in the cell (Fig. 2). Mean annual temperature was calculated by averaging the monthly temperature layer (January to December) from WorldClim version 2 (Fick and Hijmans 2017), with 1-km resolution climatic data across the global terrestrial area and computed from the historical climatic data collected during the period from 1970 to 2000. The *mean annual temperature* in each cell was extracted from the mean annual temperature layer by the coordinates of the centroid of each cell.

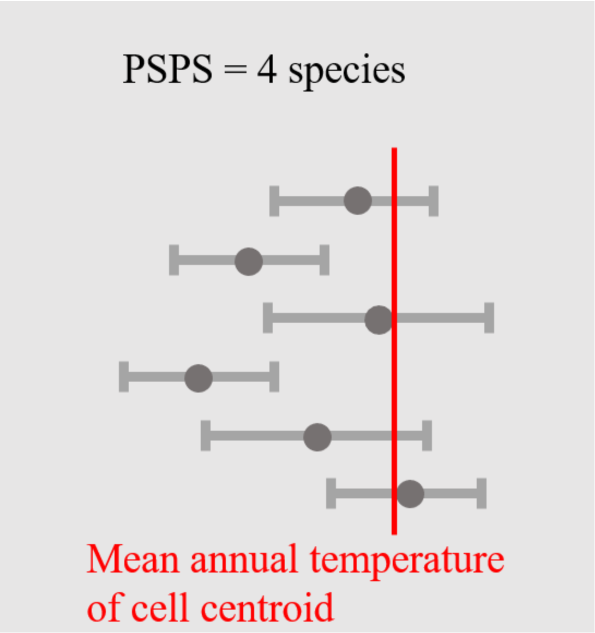

Figure 2. The conceptual diagram of potential species pool size. In this diagram, there are six species and their optimal temperature ranges (gray horizontal bars), and mean annual temperature of the cell centroid (red vertical line). Four of the species optimal temperature ranges overlap with mean annual temperature of the cell centroid; therefore, the potential species pool size (PSPS) in this example is four species.

Species preference temperature in their native ranges, which derived optimal temperature range, was calculated by averaging mean annual temperature of the location of its occurrences in its native ranges. We intersected alien species occurrences in their native ranges

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with mean annual temperature layer to extract the mean annual temperature of each species occurrence. Due to the lack of experimental design sampling, we standardized the sampling effort for GBIF occurrence data by overlapping the grid of 10 km × 10 km cells on the alien species occurrences and averaging mean annual temperatures in the same cell. To remove outliers, we only averaged the mean annual temperatures of each cell whose value fell into the 5th to 95th percentage range. The *optimal temperature range* for each alien species is the species preference temperature ± one standard deviation. *Species preference temperatures in Taiwan* were calculated in the same manner, but the size of cells for standardizing sampling effort changes to 1 km × 1 km to consider the scale difference between Taiwan and the whole world.

For human activity hypothesis, the level of human activities was approximated by the proportion of land-use type and the road density in the surrounding area of each cell. The land-use investigation map, constructed by the National Land Surveying and Mapping Center, Ministry of the Interior, R.O.C and provided by Taiwan Forestry Research Institute, was drawn based on aerial photographs during the period from 2006 to 2010. It consists of nine land-use types, of which one, agriculture, was included in further analysis. We extracted the land-use information within the buffer area between the 2-km and 1-km radius buffer areas with the centroid of each cell and calculate the proportion of agricultural land-use (Fig. 3). The road density was calculated by intersecting buffer area on the road map, derived from the land-use map. Then, we summed the length of the road within the same cell. These analyses were conducted in QGIS 3.22.14 (QGIS.org 2022).

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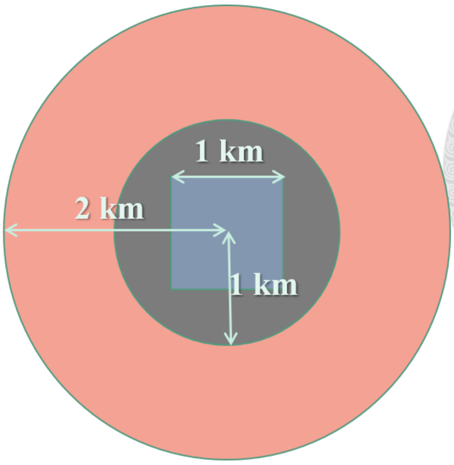

Figure 3. The buffer zone area for extracting proportion of land-use. The ring area is buffer zone. The square is the cell that was surveyed in the Survey of Invasive Alien Plants in Taiwan.

For each alien species, we attempted to derive species attributes from Wu et al. (2010):

Residence time. The residence year of each species is calculated from 2022 (this year) minus the earlier year of the first specimen and the year of the first published year.

Usage. Usage contains four categories: crop, forage, medicinal, and ornamental. We treated them as four binary variables. One species could have more than one type of usage. We applied the principal component analysis (PCA) on the species-usage matrix to extract the main gradient (usage PC1 and usage PC2) because most species have been introduced to Taiwan with multiple purposes of usage.

Bioclimatic origin. In addition to these, we also derived data about the native biome of each species. To identify the native biome of each species, we used a world biome map, based on the paper from Olson et al. (2001) and downloaded from World Wildlife Fund (Olson et al. 2001), intersecting species' native occurrences to obtain all the native biomes for each species. To avoid unequal sampling of the species occurrence, we use 10 × 10 km grids to overlap with the occurrences and select the highest count of the native biome in each grid as a record. Over all native ranges, the native biome with the most records will be the *major native biome* of one species. Because biomes are mainly made up of temperature and precipitation, and we want to verify the effect of species' temperature preference in their native ranges, we only select the temperature part of major native biome, i.e. tropical and temperate, as the *bioclimatic origin* for further analysis.

Statistical analyses

We analyzed three kinds of alien species richness-elevation patterns: all habitats, roadside habitats, and agricultural habitats. To make the species richness comparable among cells, we first conducted plot-based rarefaction and extrapolation to standardize sampling effort for all the habitats within the cell (for all habitats alien species richness-elevation pattern) or each habitat type within each cell (for roadside and agricultural habitat types) to five plots by R package *iNEXT* (Chao et al. 2014, Hsieh et al. 2016). We chose to standardize to five plots per cell since Chao and Jost (2012) suggested that this method can extrapolate to twice the number of plots.

To describe the alien species richness-elevation pattern, we conducted smooth spline to fit the alien species richness-elevation pattern. We conducted multiple linear regression and variation partitioning on standardized species richness with two categories of variables, potential species pool size and land-use, to discover their partial effects and share effects with the function *varpart* in R package *vegan* (Oksanen et al. 2020). The standardized species richness and land-use variables are square-root transformed to fulfill the linearity assumption. We displayed the explained proportion of a variable category by the adjusted R squared. We tested the partial effects of these two hypotheses by partial F test.

To explore how important the species temperature requirements are to the alien species in Taiwan, we included all the alien species in the Taiwan island regardless of the habitats they located in the Survey of Invasive Alien Plants in Taiwan dataset. We excluded the species whose number of occurrences (see *Alien species occurrences* section) in their native ranges or Taiwan are too few (less than five occurrences) to represent the temperature preference of this species (Appendix 2).

We conducted Pearson's correlation analysis on the species preference temperature in their native ranges and temperature preference in Taiwan island. We also plotted 396 species' preference temperatures in their native ranges and Taiwan on the scatter plot and drew an identity line (a line with a slope of one and intercept zero) to visualize the matches. The *temperature deviations* for individual species were quantified as the difference between the species preference temperature in Taiwan and species preference temperature in their native ranges. A positive difference represents species that on average occur in Taiwan in warmer locations than in their native ranges. We attempted to explain the temperature deviations of temperature preference in Taiwan from temperature preference in their native range by attributes of alien species, namely by their major native biome, residence time, and usage.

To evaluate the distribution of alien species along elevation, we used the alien species occurrences in Taiwan to extract the elevation that alien species reside in and remove extreme elevation records of each species by excluding values out of 5th to 95th percentage, and calculated the elevation length by elevation maximum minus elevation minimum.

Results

Cell-level analyses

The number of alien species per cell, standardized by rarefaction to five plots, ranges from 0.5 to 39 in the whole dataset, from 1 to 40 in the roadside habitat, and from 4 to 46 in the agricultural habitat. There were on average 14.7 ± 0.2 (mean ± SE), 14.2 ± 0.2 and 16.49 ± 0.3 alien species per cell in the cell without being selected by habitat types, the roadside and agricultural habitats, respectively. The alien plant species richness-elevation patterns are decreasing in the whole Taiwan and also in roadside and agricultural habitats. In the whole dataset, alien species richness stays the highest in the lowland, decreasing sharply between 500 m to 1500 m, and the slope becomes flatter after 1500 m (Fig. 4a). The shapes of alien species richness-elevation patterns in these two habitat types were similar to that of pattern in Taiwan (Fig. 4b and 4c), but the alien species richness decreases earlier in the lowland of agricultural habitat than that in the whole dataset. The variance of species richness changes along the elevation gradient, with large variance in the lowland and small variance in mountain ranges (Fig. 4a, 4b and 4c).

For the species temperature preference hypothesis, we derived potential species pool size for every cell in the Survey of Invasive Alien Plants in Taiwan based on the mean annual temperature. The trend of potential species pool size along the mean annual temperature were similar in roadside and agricultural habitats (Fig. S1a). Potential species pool size in roadside habitat is a little larger than that in agricultural habitat. We found that potential species pool size was in proportion to mean annual temperature when mean annual temperature was within the 5th to 95th percentage range of mean annual temperature in each cell. The highest potential species pool size occurs around 23℃. Then potential species pool size decreases sharply to zero over 25℃ (Fig. S1a). The trend of potential species pool size in roadside and agricultural

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habitat decrease as elevation increase means the species availability in lowland is higher than that in mountain ranges (Figs. S2a and S2d).

For human activity hypothesis, we use the proportion of the agricultural land-use and road density in the buffer zone of the cells to represent different kinds of impacts from human activities. In both roadside and agricultural habitats, these two variables are moderately correlated with the elevation gradient in a negative relationship (Fig. S3).

The decreasing alien species richness-elevation patterns in roadside and agricultural habitats are explained more by the potential species pool size, whose partial adjusted R^2 are 0.081 and 0.074, respectively (Table 1 and Fig. 5). The land-use variables explain less variance individually, with partial adjusted $R^2 = 0.031$ in roadside habitat and without any significant marginal effect in agricultural habitat (Table 1 and Fig. 5). The potential species pool size and land-use variables jointly explain more variance of alien plant species richness in the roadside (adjusted $R^2 = 0.171$) than in agricultural habitat (adjusted $R^2 = 0.095$). In both roadside and agricultural habitats, potential species pool size and land-use variables share a relatively large portion of variance (Fig 5a and 5b).

Species-level analyses

We tested if the species' temperature requirements in their native ranges are important to their distribution along the temperature gradient in Taiwan. From 396 alien species, most of the alien plant species (257 species, 65% of all the alien species) in our analysis match their temperature requirements in their native range, with their preference temperature deviations not more than 3°C (Table 2). There is a strong correlation between the species preference temperature in their native ranges and Taiwan ($r = 0.67$, $P < 0.001$). However, the other 139 species in our analysis did not match their temperature requirements (temperature deviation is more than 3°C). One

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hundred and seven of them occur in warmer locations in Taiwan than in their native ranges (Table 2 and Fig. 6a, the data points above the identity line). The species native to less than 15°C do not reach as cold as their native ranges and most of them are species of temperate origin (Fig. 6a). The species native to warmer than 25°C do not reach the habitats as warm as their native ranges and most of them are species of tropical origin (Fig. 6a).

We further explored the species attributes of those with higher temperature deviations between Taiwan and their native ranges. We found that the species with higher temperature deviation mostly are temperate origin with non-ornamental usage. We grouped alien species by their bioclimatic origin (Table 3, adjusted $R^2 = 0.569$, $P < 0.001$). Temperature deviations of species of temperate origin are significantly higher than that of other origin biomes (Figure 6b and S4, $P < 0.001$). We narrow down the scale of bioclimatic origin into major native biome. Major native biome is the best explanatory variable of temperature deviation (Table 3; adjusted $R^2 = 0.623$, $P < 0.001$). Temperate broadleaf and mixed forests have the highest temperature deviation, which means the species that originated in this biome mostly occur in warmer habitats in Taiwan than their native ranges. The species of temperate origin have larger temperature deviation than species of tropical origin (Fig. 7 and Table S5). The residence time of alien species is not related to the temperature deviation (Fig. 8 and Table 5; $P > 0.05$). For economic usages, the PCA diagram (Fig. 9a) shows that the first principle component axis represents the ornamental usages (representing 47.7% variation of the alien species), while the second axis is related to medicinal usage (representing 29.6% variation of the alien species). Only the first axis score (ornamental use) has a significantly, negatively weak relationship with the temperature deviation (Fig. 9b, adjusted $R^2 = 0.021$, $P < 0.05$).

Most of the alien species occur in the elevation gradient range from lowland to some extent (Fig. 10a). Medians of elevation distribution for each species mostly are closer toward lowland (Fig. 10a). Species in the higher elevation mainly composed of species with larger elevation ranges, i.e., temperature generalists (Fig. 10b). Species with higher elevation maximum mostly are species of temperate origin, while species in the lowland are species of tropical origin (Fig. 10b).

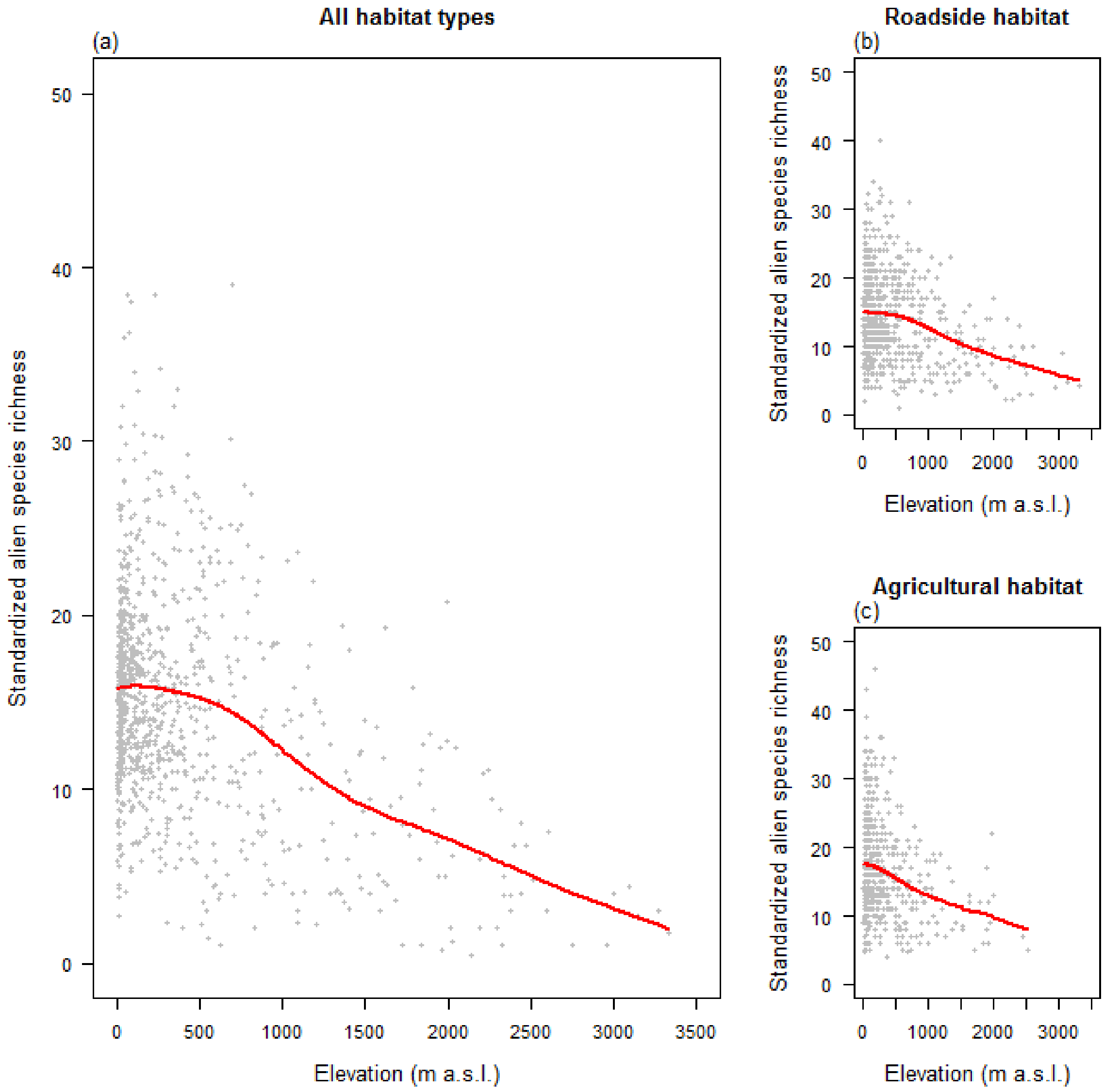

Figure 4. Alien species richness-elevation pattern in (a) all habitat types, (b) roadside habitat and (c) agricultural habitat. These patterns are shown by smooth spline. Alien species richness is standardized to five plots per grid.

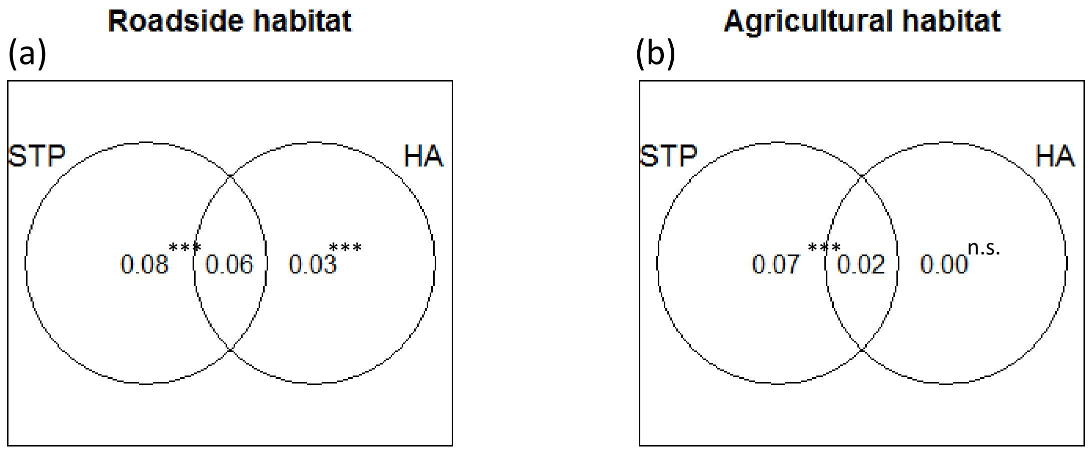

Figure 5. Venn's diagram for variation partitioning on the standardized alien species richness, is explained by potential species pool size and land-use variables in the roadside and agricultural habitats. STP: Species temperature preference hypothesis (includes potential species pool sizes). HA: Human activity hypothesis (includes land-use variables, the proportion of agriculture area and road density in the buffer zone of the cell centroid). The numbers in each fraction are the adjusted R^2 explained by variables in that fraction. Levels of statistical significance are indicated as: * for $P < 0.05$, ** for $P < 0.01$, ***for $P < 0.001$, and n.s. for $P \geq 0.05$.

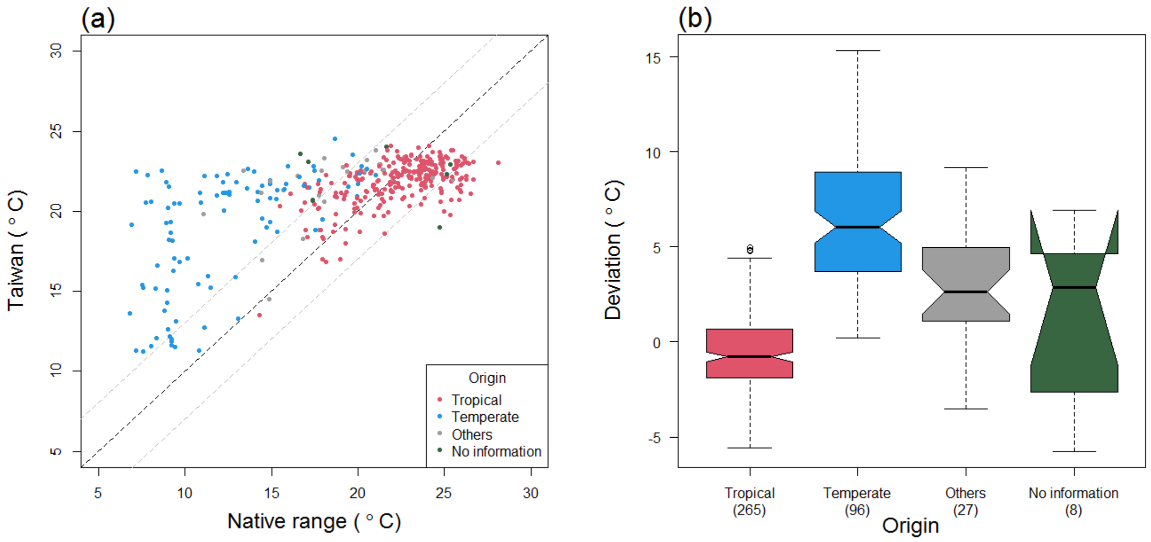

Figure 6. (a) The correlation between the species preference temperature in their native range and Taiwan. (b) The comparison of temperature deviation with their bioclimatic origin. A dot means one alien species. A black dash line is an identity line with a slope of one and no intercept. Gray dash lines represent the boundaries of temperature deviation within ± 3°C. The colors of dots and boxes indicate the major origin of the alien species. No information refers to species without native biome information. The numbers in brackets are the number of species that are mainly native to certain biome.

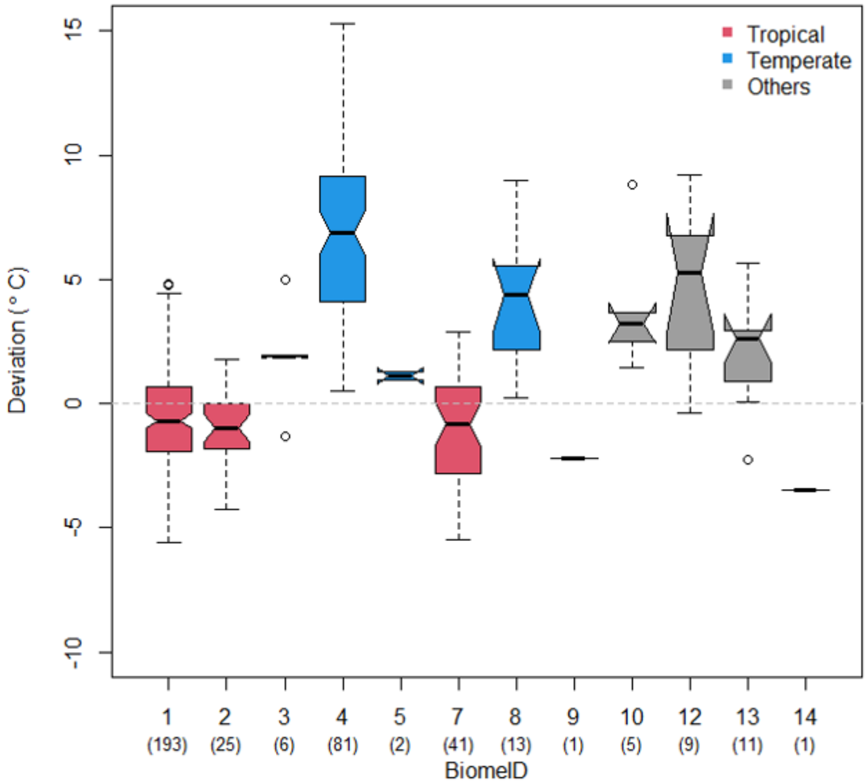

Figure 7. The comparison of species preference temperature deviation between their native range and Taiwan with their major native biomes. The numbers in brackets are the number of species that mainly native to certain biome. 1: Tropical and subtropical moist broadleaf forests. 2: Tropical and subtropical dry broadleaf forests. 3: Tropical and subtropical coniferous forests. 4: Temperate broadleaf and mixed forests. 5: Temperate coniferous forests. 7: Tropical and subtropical grasslands, savannas, and shrublands. 8: Temperate grasslands, savannas, and shrublands. 9: Flooded grasslands and savannas. 10: Montane grasslands and shrublands. 12: Mediterranean forests, woodlands, and scrub. 13: Deserts and xeric shrublands. 14: Mangroves.

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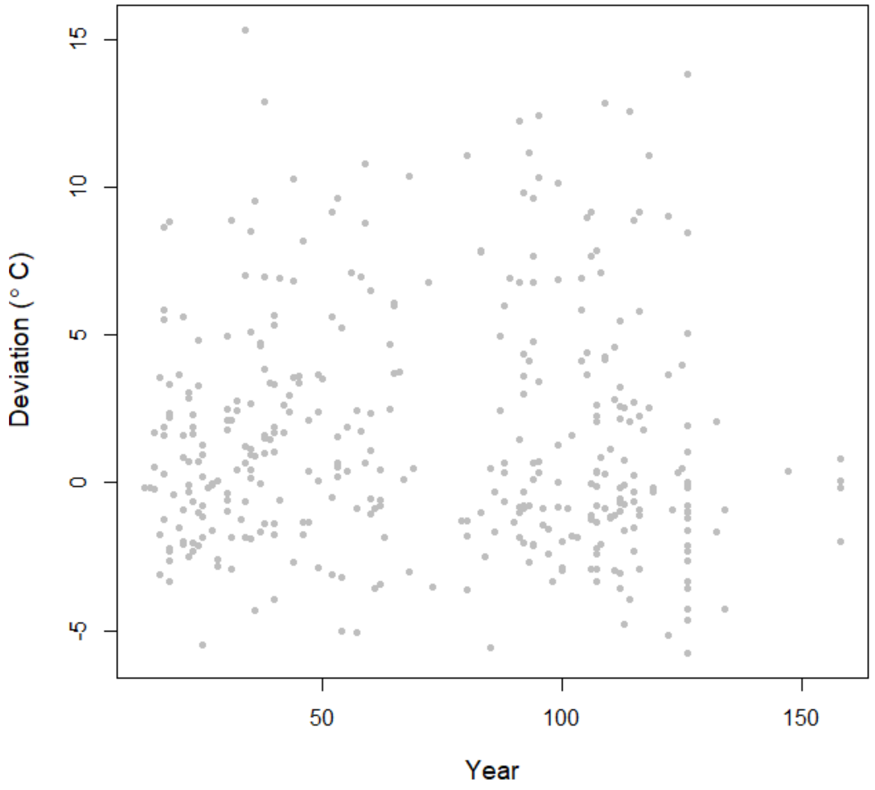

Figure 8. The scatter plot of the species preference temperature deviation between their native range and Taiwan and the residence time.

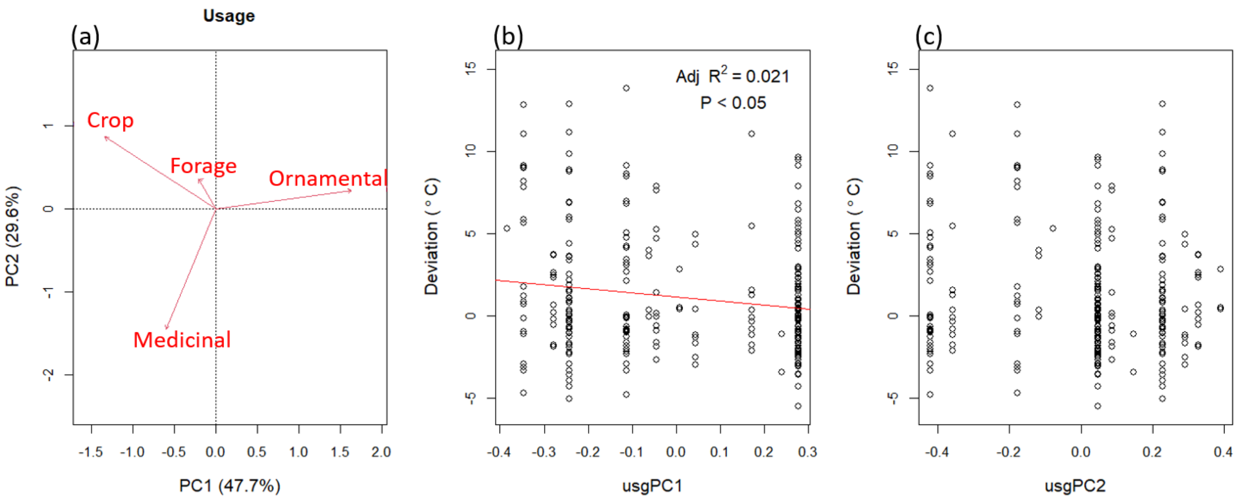

Figure 9. PCA ordination of the economic usage of alien species (a) and the regression of the species preference temperature deviation between their native ranges and Taiwan on the first (b) and the second principal axes (c). Significant relationship (P < 0.05) is shown by red line.

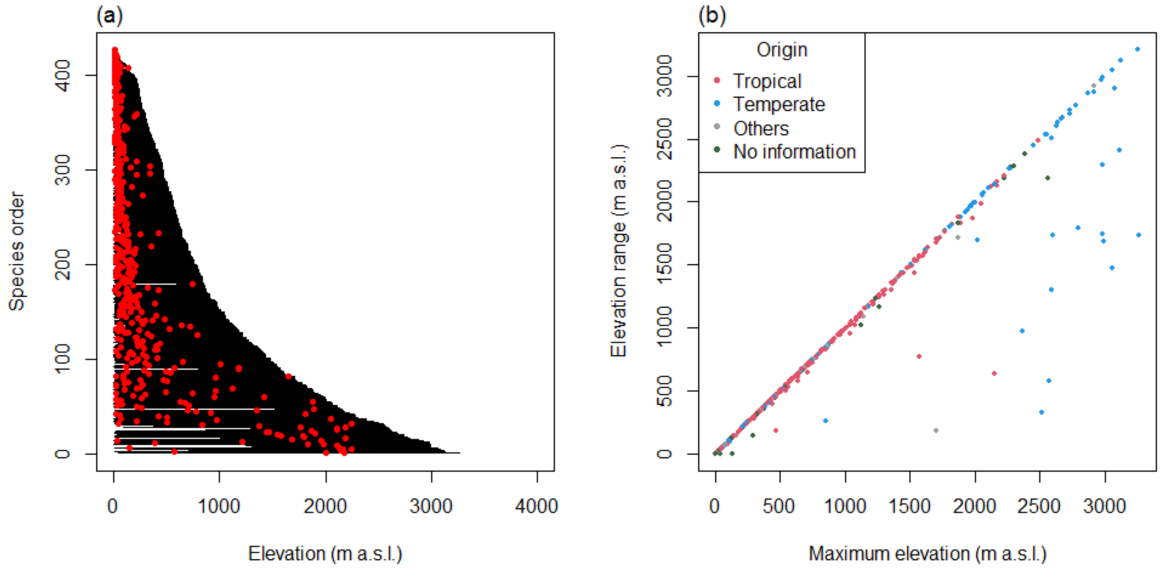

Figure 10. (a) The elevation range (black lines) and median elevation (red dots) of alien species occurrence in Taiwan, vertically ordered by maximum elevation of occurrence (highest at the bottom). (b) The relation between the elevation range and the maximum elevation of alien species in Taiwan (one dot represents one alien species). Each point was colored by their bioclimatic origin.

Table 1. The table of statistics for each segment of variation portioning of alien species richness on potential species pool size and land-use variables in roadside and agricultural habitats. STP: Species temperature preference hypothesis (includes potential species pool sizes). HA: Human activity hypothesis (includes land-use variables, proportion of agriculture and road density in the buffer zone of the cell centroid). STP w/o HA: partial effect of STP. HA w/o STP: partial effect of HA.

Habitat type	Factor	adj R^2	F value	P-value
Roadside	STP	0.141	128.3	< 0.001
	HA	0.090	39.39	< 0.001
	STP+HA	0.171	54.55	< 0.001
	STP w/o HA	0.081	77.123	< 0.001
	HA w/o STP	0.031	15.287	< 0.001
Agriculture	STP	0.091	51.79	< 0.001
	HA	0.020	6.313	0.002
	STP+HA	0.095	18.68	< 0.001
	STP w/o HA	0.074	42.375	< 0.001
	HA w/o STP	0.004	2.0191	0.134

Table 2. The table of the number of alien species following the temperature preference in each bioclimatic origin group. The numbers in the parentheses are the proportion of the number of the species of the species that belongs to certain bioclimatic origin and the level of temperature preference shift. The temperature deviations were calculated by the mean annual temperature in Taiwan minus that in the native range of alien species.

	All species	Tropical species	Temperate species
Number of species	396	265	96
Temperature deviation > 3	107 (27.0%)	12 (4.5%)	80 (83.3%)
Temperature deviation < -3	32 (8.1%)	30 (11.3%)	0 (0.0%)
|Temperature deviation| < 3	257 (64.9%)	223 (84.2%)	16 (16.7%)

Table 3. The statistic table of regressing temperature deviation to species attributes.

	Number of species	Adjusted R^2	P-value
Native biome	388		
Bioclimatic origin		0.569	< 0.001
Major native biome		0.623	< 0.001
Residence time	376	-0.002	0.572
Usage	252		
1st usage PCA axis		0.021	0.013
2nd usage PCA axis		0.004	0.151

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Discussion

Our study shows that, the alien species richness-elevation pattern is monotonically decreasing in Taiwan, which agrees with decreasing alien species richness-elevation patterns found in other parts of the world (Guo et al. 2018). Studies dealing with the decreasing alien species richness-elevation pattern mainly focused on Europe and the Americas, but are seldom conducted in Asia (Pyšek et al. 2008). Our finding is similar to that from central Japan, with decreasing alien species richness along with increasing elevation (Tanaka & Sato 2016).

Species temperature preference hypothesis explains more variance in alien species richness-elevation pattern in Taiwan than the human activity hypothesis. Pyšek et al. (2010) conducted a continental-scale analysis focused on explaining the relative importance of alien species within different regions of the world and used climatic and land-use variables to quantify the relative importance of climatic parameters and human activities. The authors found that climatic variables are stronger predictors of alien species richness than human activity. Their study is similar to ours in the methods of analysis (variance partitioning), although the main hypothesis being tested is not focused on the elevation-richness relationship.

However, the large shared amount of variance explained by both species temperature preference hypothesis and human activity hypothesis brings uncertainty in the interpretation of analysis results. The shared fraction of explained variance is caused by the correlation of both sets of variables (human activities are more intensive in lowlands with higher temperatures and larger species pool of alien species), and it makes not possible to show which hypothesis is more influential. To solve the ambiguity of the interpretation of the variation partitioning results, we compared the species preference temperature between Taiwan and their native ranges to find more persuasive evidence. We found that 65% of the alien species in Taiwan follow their temperature preference in their native range. The pattern implies there are some reasons to make alien species from all over the world follow the same rule, tending to colonize habitats with the temperature similar to their native range. This supports the importance of climate matching for the naturalization of alien species. Alien species should pass the environmental and reproductive barriers to become naturalized (Richardson et al. 2000b; Richardson & Pyšek 2012). The environmental barriers include climatic factors in the introduced ranges, which control the survival of the alien species. Some studies using climate-based niche models report that climatic matching of alien species between native and introduction regions enhances invasion success (Panetta & Mitchell 1991; Thriller et al. 2005).

However, the climatic niche shift, the shift of the climate where the species are able to establish a stable population in their introduced ranges (Atwater et al. 2018), is still prevailing among Taiwan’s alien species. Nearly 40% of species do not follow their species preference temperature. Actually, climatic niche shifts are common in the alien species globally (Atwater et al. 2018). In our study, most of the species with higher temperature deviation from their native range are species of temperate origin. Janzen (1967) proposed a hypothesis to link the variation of native climate (temperature) of species to their physiological difference and biogeographic patterns. Species of temperate origin experience seasonality in their native ranges and they have evolved to adapt to broader thermal ranges with similar summer temperatures and much colder winter temperatures than the species experienced in the tropical region. In contrast, tropical regions’ thermal amplitude is less variable than in those of temperate regions across seasons. Thermal tolerance ranges of species of tropical origin are thus narrower than species of temperate origin. As a result, the steep temperature gradient along elevation is not an obstacle for the distribution of species of temperate origin, but it is an obstacle for species of tropical origin. Hence, the distribution range of temperate-origin species would be wider than that of tropical-origin species. The pattern would be more pronounced for plants since plants have lower mobility to escape from unfavorable conditions and need to deal

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with the local climate directly (Huey et al. 2002). Thus, we can find some species of temperate origin which could survive in lowlands where the ambient temperature is warmer than in their native ranges, which results in larger temperature deviation. However, we do not have evidence that can show that temperate species have broader thermal tolerance ranges in our study.

Residence time of alien species has been reported to be positively related to their dispersal, so it increases the possibility of alien species dispersing to their suitable habitats as the residence time gets longer (Pyšek and Jarošík 2005). Thus, when alien species spread across larger area, the species preference temperature in the introduced range would approach the species preference temperature in their native range, and the temperature deviation of alien species between their native ranges and introduced range would diminish. Surprisingly, the residence time does not show a significant relationship with the temperature deviations in our study. The reason might be the data quality of the proxy we used to represent residence time. The time of the first record, which was defined as the earliest year of the first herbarium record or documentation, is not necessarily the same as the time alien species being introduced. Some species have been introduced to Taiwan for hundreds of years but were first recorded within the last two hundred years. For example, *Euphoria longana* was introduced to Taiwan in the 17th century (Shen 1774), but the record of its first introduction is in 1911 in our dataset.

Our analysis has shown that in Taiwan, alien species with non-ornamental usage usually grow in habitats warmer than in their native ranges, while species of ornamental usage usually occupy habitats that better fit their temperature optima. The economic usages imply the selection of alien species' traits. Humans select plants with commercial values for ornamental usage (e.g., fast vegetative growth, long flowering period, repeated bouts of flowering, good pest resistance and good adaption to several climates), and those traits coincidently promote invasiveness (Mack 2005; Hulme, 2011; Reichard 2011). Ornamental plants have the highest naturalization success among economic usages (van Kleunen et al. 2020). Those ornamental usage plants might be easier to reach their suitable habitat in the introduction ranges because of their good ability to disperse, reproduce and acclimate. Humans also actively plant them, by spreading their propagules in gardens, roadside and other places, which enhances the possibility of naturalization of ornamental plants. As a result, these species may occupy more suitable habitats with temperatures close to their native ranges. On the contrary, species with non-ornamental usage (medicinal) were possibly selected for their quality instead of quantity (van Kleunen et al. 2020). They have less naturalization success than ornamental plants (van Kleunen et al. 2020), so they could not occupy their suitable niches as fast as ornamental plants. This may explain why they reside in warmer habitats in Taiwan than in their native range.

However, the comparison of species preference temperature between Taiwan and their native ranges can be biased if Taiwan does not provide the same temperature range as their native ranges. Even if the alien species occupy all the habitats with the temperature within their native temperature range in Taiwan, the species preference temperature in Taiwan would not be the same as their native ranges resulting in temperature deviations.

Additionally, we found that most of the alien species in Taiwan are distributed from lowlands to certain elevations, and only a few species are specialists in higher elevations. This phenomenon was also found by Alexander et al. (2011) in different regions of the world. In their study, most of the alien species in the higher elevation are species with broad climatic amplitudes, and those species are the generalists in the elevation gradient. They were introduced from the lowlands and gradually migrated to higher elevations along steep temperature gradients. Alexander et al. (2011) named the decreasing alien species richness-elevation pattern which is caused by filtering lowland species pool “directional ecological filtering”. We think this pattern shows that alien species mainly disperse from lowlands to higher elevations in Taiwan and indicates that alien species richness-elevation patterns are shaped by the species temperature preference and human activities jointly.

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Aside from exploring the possible reason of alien richness-elevation pattern by the main two hypotheses, we also found some linkage between the elevation-richness pattern and the effect of habitat type. Land-use variables (proportion of agriculture and road density in the buffer area) hardly explain any variance of alien species richness in agricultural habitats. On the other hand, land-use variables explained a portion of the variance in species richness in some of the roadside habitats. Roadside is considered to be the corridor, a long, relatively connected and disturbed site, making it easy for dispersing of alien species (Tikka et al. 2001; Mortensen et al. 2009; Paiaro et al. 2011). In Ohio, USA, the study of Christen and Matlack (2009) found that roadside functions as a habitat and corridor for alien species to spread. Roadside provides habitats with high availability of light that stimulates alien species germination and improves their vegetative growth. At the same time, the dispersal along the road is higher than that in the perpendicular direction. Not only could roadside itself promote dispersal of alien species richness, but the vehicles also running through the road facilitate long-distance dispersal by carrying a large number of seeds (von der Lippe and Kowarik 2007). This study, conducted in a single motorway in Berlin, Germany, reported that the annual seed rain brought by vehicles ranged from 635 to 1579 seeds per meter square per year, in which alien plants accounted for half of the species and the number of seeds (von der Lippe and Kowarik 2007). The neighborhood region provides propagules to the roadside and then alien species spread and take the advantage of the roadside for good dispersal (Pauchard and Alaback 2004). As a result, the occurrence of land-use types near the roadside habitat plots is crucial for the alien species richness in these habitat plots. In contrast, species richness in the agricultural habitat plots is not closely related to the land-use types of surrounding agricultural habitat plots. The possible reason may be that the agricultural habitat itself served as the source of propagules for alien species. Hence, the temperature is the main determinant of alien species richness in agricultural habitats.

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The reason why human activity hypothesis explains less variation with insignificant results might cause by the following reasons. Some human-related factors that might influence the species richness pattern were not included in our study. For example, factors related to species ability to cross the geographic barrier, such as trade and tourism, which promote the immigration rate of alien species. Human demographic factors, such as population size and density, and socio-economic factors, such as per capita gross domestic product and other national wealth estimates. Both of them are a proxy for various human impacts on the ecosystem. The common human impacts include modifying natural habitats, removing the native vegetation, and enhancing the propagule pressure of alien plants. Some studies have found that those human-related factors are positively related to alien species richness (Dawson et. al 2017; Spear et al. 2013). Vilà and Pujadas (2001) found that the density of alien plants in European and North African countries was best explained by imports and Human Development Index, an indicator of human development in health, knowledge, and standard of living. Distances from putative sources (like cities, harbors and airports) are often used as surrogates of the propagule pressure and researchers found them important to explain the alien species richness (Timmins and Williams 1991; Alston and Richardson, 2006; Bellard et. al 2016). However, human-related factors mentioned above are merely just indirect surrogates of propagule pressure and anthropogenic disturbance, and may have no direct relationship with the possibility of alien species introduction, naturalization and dispersal.

The factors promoting the invasion of alien plants differ depending on the invasion stage at which species occurs. For the alien species in the introduction stage, factors related to crossing the geographic barrier and making it easier to adapt in the introduced range are more influential than other factors (Richardson and Pyšek 2012). In the naturalization stage, the factors that influence the sustainable reproduction of alien plants in the habitat play a major role in their invasion success (Richardson and Pyšek 2012). During the invasion stage, dispersal

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traits and the ability to invade natural and seminatural habitats become the determinant factors mediating invasion success (Richardson and Pyšek 2012). We can expect that in our dataset, different species are currently at different invasion stages. Hence, the response of alien species in the naturalization stage to the land-use variables (proxies for propagule pressure) is masked by processes dominating the other stages.

The current number of alien species does not necessarily reflect the impact of recent factors. Introduced species cannot spread to all the suitable habitats when they were first introduced to a new region. This means there is a time lag between the contemporary human-related factors and the recent patterns of alien species richness, called “invasion debt”. Current invasion conditions can be the result of historical human activities. Essl et al. (2010) pointed out that the historical socio-economic activities in 1900 explained more variance of the current pattern of alien plant species richness in Europe than the same set of human-related factors in 2000. Mattingly and Orrock (2013) conducted an experiment on post-agriculture land and remnant habitat and found that past land-use would affect the establishment success of invasive plants and their response to water and nutrition addition. In our study, our land-use factors were collected near the time when the species occurrence data were collected. This could be part of the reasons why the human activity hypothesis does not explain as much variance as our expectation.

There are some limitations of our study which can be improved in the future. First, we used mean annual temperature of each alien species occurrence as the species preference temperature. Using mean annual temperature cannot differentiate the temperature between places that have different temperature variation but the same mean annual temperature, a situation that implies different temperature preference. Choosing minimum temperature of growing season instead of the mean annual temperature may have a better ecological meaning. Second, the sampling design of the dataset we are using may not be very suitable for studying

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alien species richness-elevation pattern, since the sampling distribution of cells is highly skewed toward lowlands, with only few cells in high elevations. As a result, the species temperature preference temperature in Taiwan may be biased toward warmer temperatures, resulting in larger species preference temperature deviation between Taiwan and their native ranges. Third, we have not distinguished alien plants according to their life history in our analysis. Annual plants survive the unfavorable season in dormancy, so they may not be sensitive to the temperature in the winter. In contrast, perennial plants should tolerate the lowest temperature, although some may escape it by retaining only underground parts during the coldest season. As a result, different life history might react differently to temperature and it may be better to analyze their preference temperatures separately.

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Conclusions

In Taiwan, the plant species richness of alien species is monotonically decreasing along the elevation gradient, and this pattern is mainly explained by species temperature preference hypothesis. More than half of the alien species match their temperature preference between Taiwan and native ranges, demonstrating the importance of niche conservatism in the invasion. Most of the species with matching temperature preferences are species of tropical origin, usually occurring in lowlands, i.e., in habitats whose temperatures are similar to that in their native ranges. Temperate species mostly reside in the warmer habitats in Taiwan compared to their native preference temperature. Thus, they could occur in both lower and higher elevations. This pattern may be not only because the habitats which match their preference temperature in native ranges are in the higher elevations, but also because they tend to be introduced from the lowlands and need more time to migrate to higher elevations. In our study, human activity hypothesis explains less variation then species temperature preference hypothesis. It could be due to the data limitation of proxy of the propagule pressure or invasion debt. The importance of human activity should be further investigated. We conclude that alien species in Taiwan spread from lowlands to higher elevations and are gradually filtered out by the temperature gradient of mountains based on their species temperature preference in their native ranges. Consequently, the size of the alien species pool decreases along the elevation gradient resulting in decreasing alien species richness elevation pattern.

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Appendices

Appendix 1: Supplementary results

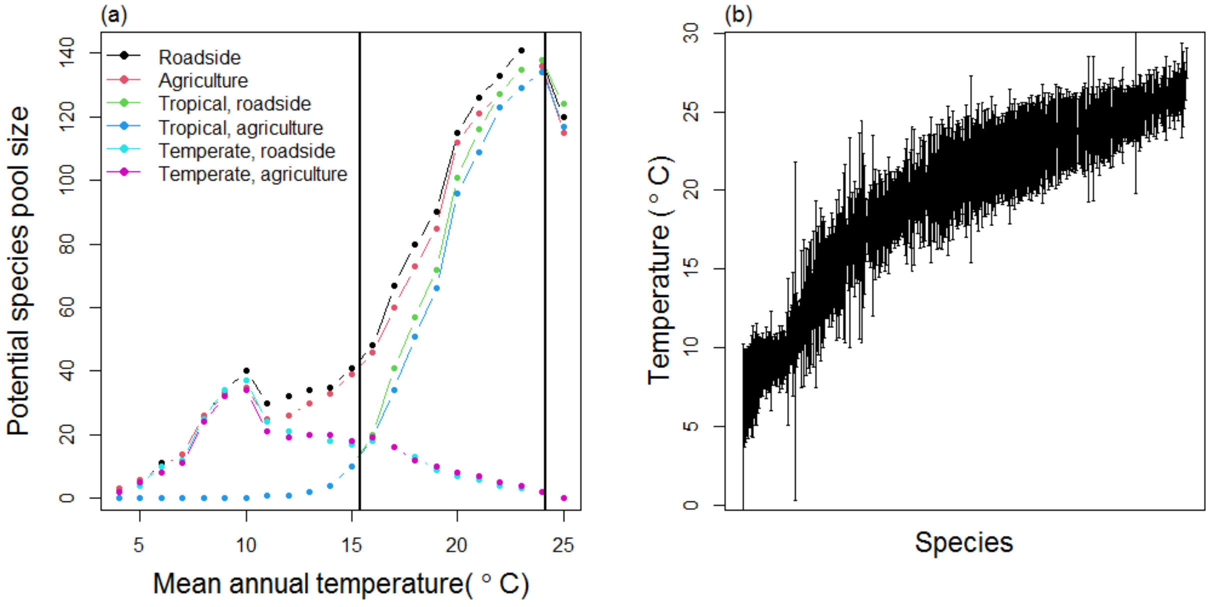

Figure S1. (a) Potential species pool size changes along mean annual temperature. This figure displays the potential alien species pool size in Taiwan which was calculated from the mean annual temperature of each species. The range of mean annual temperature is the range of mean annual temperature of the cell centroid in Survey of Invasive Alien Plants in Taiwan, and two black lines indicate 5 to 95% of the range of the mean annual temperature among the cells in Survey of Invasive Alien Plants in Taiwan. (b) Species optimal temperature ranges in their native habitats for all the species in Survey of Invasive Alien Plants in Taiwan, sorted along the x-axis by preference temperature of each species.

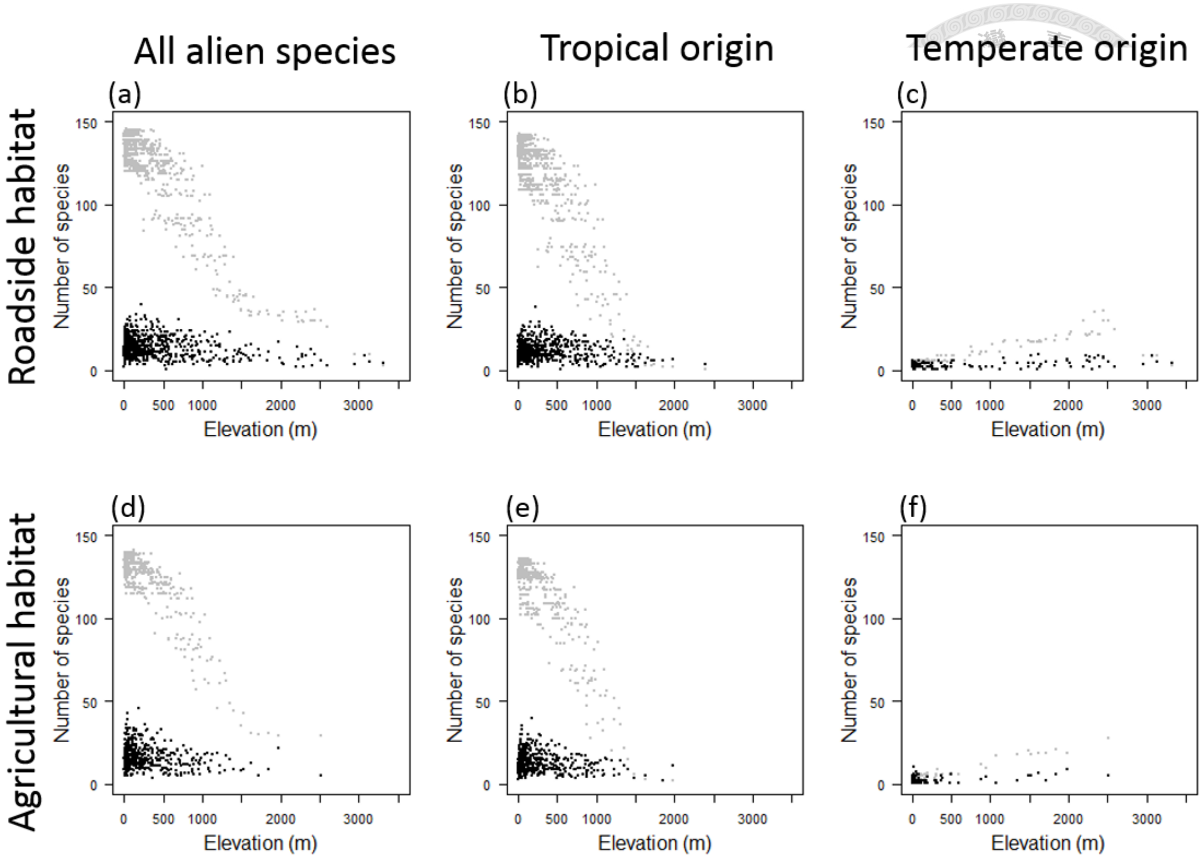

Figure S2. Potential species pool size (grey dots) and standardized species richness (black dots) of alien species in roadside habitats (upper row) and agriculture habitats (lower row), projected against the elevation gradient. The pattern is displayed for all species (left column), and only a subset of tropical origin species (middle column) and temperate origin species (right column).

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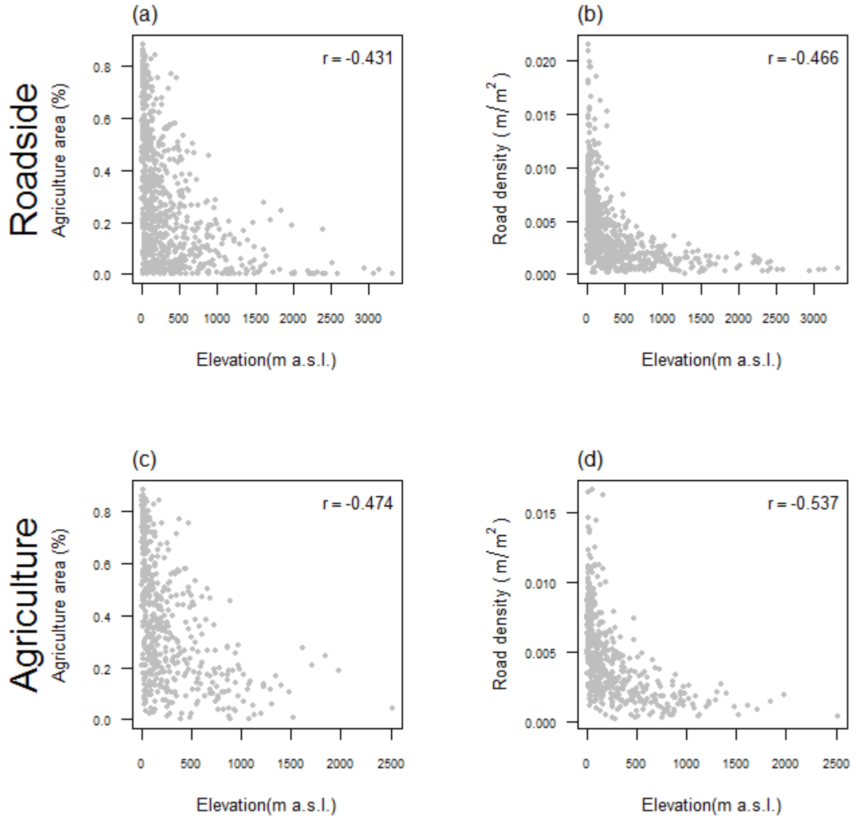

Figure S3. The scatter plots of the correlation between elevation and the proportion of agriculture land-use and road density in the buffer zone in roadside and agricultural habitat types. Pearson’s correlation coefficients were shown in the figure.

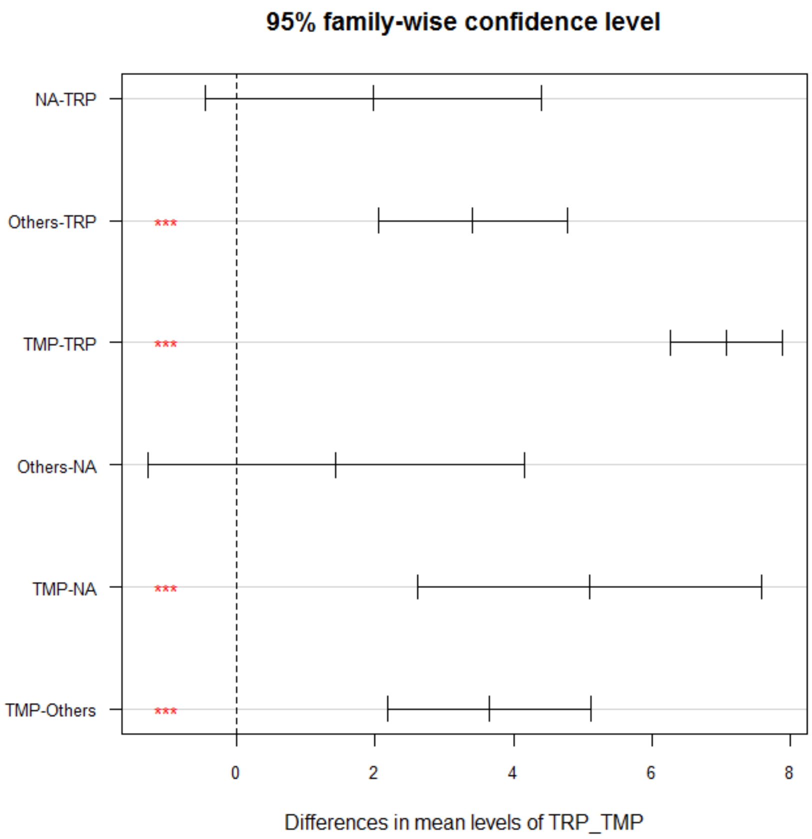

Figure S4. The differences in observed means of temperature deviations for each pair of bioclimatic origin and 95% confidence interval of the differences. TMP: Temperate origin. TRP: Tropical origin. Others: Other bioclimatic origins. NA: No bioclimatic origin information. The significance of the differences in each pair of biomes is tested by the Tukey test. Levels of statistical significance are indicated as * for $P < 0.05$, ** for $P < 0.01$, and *** for $P < 0.001$.

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Figure S5. The differences in observed means of temperature deviations for each pair of biomes and 95% confidence interval of the differences. The significance of the differences in each pair of biomes is tested by the Tukey test. Levels of statistical significance are indicated as * for P < 0.05, ** for P < 0.01, and *** for P < 0.001.

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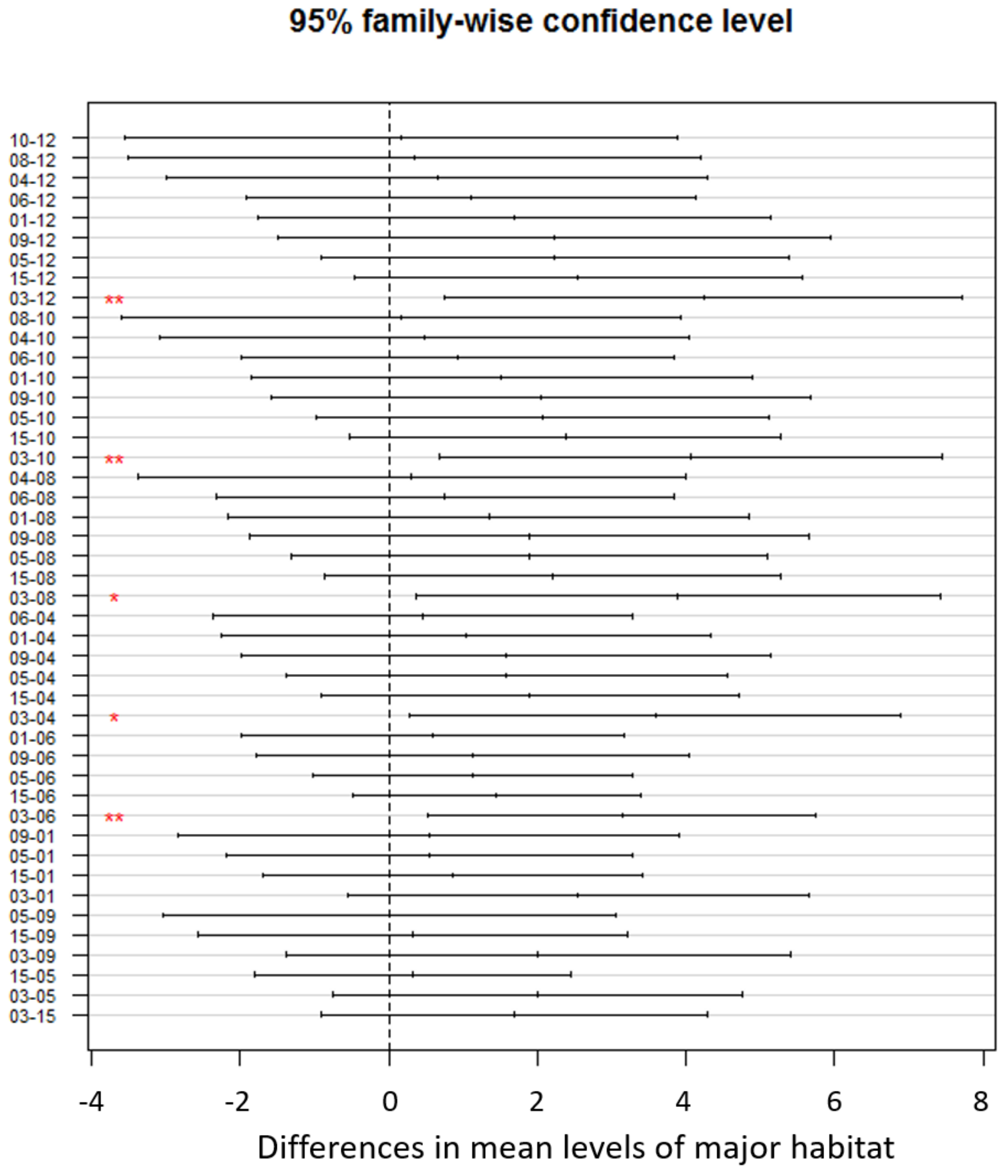

Figure S6. The differences in observed means of temperature deviations for each pair of major habitat types and 95% confidence interval of the differences. The significance of the differences in each pair of biomes is tested by the Tukey test. Levels of statistical significance are indicated as * for $P < 0.05$, ** for $P < 0.01$, and *** for $P < 0.001$. 01: Roadside. 03: Agriculture land. 04: Orchard. 05: Abandoned farm land. 06: Abandoned grassland. 08: Natural forest. 09: Forest plantation. 10: Bamboo forest. 12: Waterfront. 15: Artificial construction.

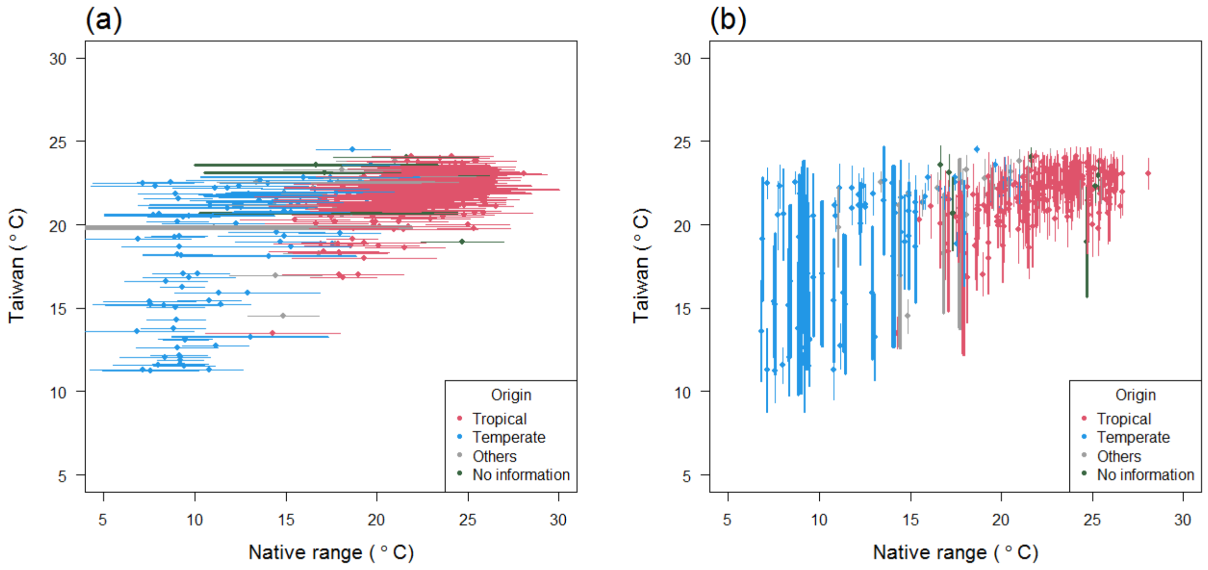

Figure S7. Compare the species' niche width in (a) their native ranges and (b) Taiwan. Species niche width was calculated by species preference temperature ± one standard deviation.

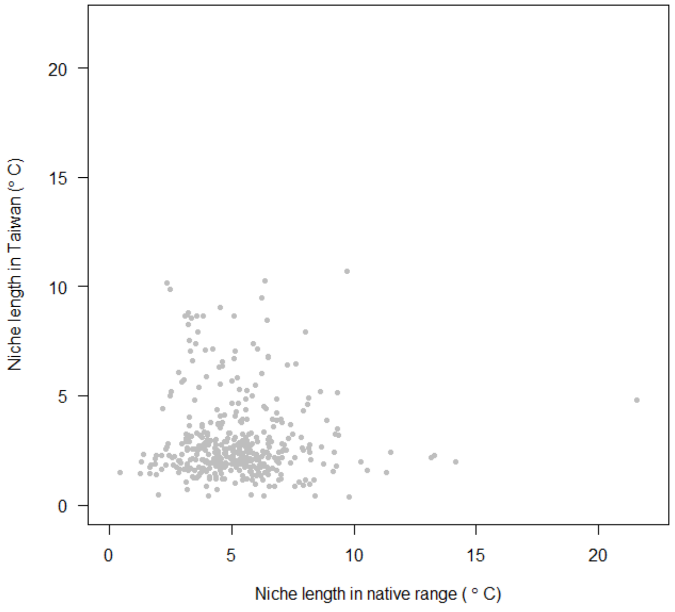

Figure S8. Correlation plot of niche length along the temperature gradient in Taiwan and their native range. Their correlation is not significant (P > 0.05).

Appendix 2: Species name list for each analysis

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Table S1. The list of species names used in each analysis.

Species	VPRD	VPAG	SPT	B	RT	U
Abelmoschus moschatus	-	+	+	+	+	+
Abutilon crispum	+	-	+	+	+	-
Abutilon striatum	-	-	+	+	+	+
Acacia farnesiana	-	+	+	+	+	+
Acalypha indica var. *indica*	+	+	+	+	+	+
Acmella brachyglossa	-	+	+	+	+	-
Acmella paniculata	+	-	+	+	+	-
Acmella uliginosa	-	+	+	+	+	+
Aeschynomene americana var. *americana*	+	+	+	+	+	+
Agave sisalana	-	-	+	+	+	+
Ageratum conyzoides	+	+	+	+	+	+
Ageratum houstonianum	+	+	+	+	+	+
Albizia lebbeck	-	-	+	+	+	+
Alopecurus myosuroides	+	-	-	-	-	-
Alstonia scholaris	-	-	+	+	+	+
Alternanthera bettzickiana	+	+	-	-	-	-
Alternanthera paronychioides	+	+	+	+	+	+
Alternanthera philoxeroides	+	+	+	+	+	+
Alternanthera sessilis	+	+	+	+	+	-
Alysicarpus ovalifolius	+	+	+	+	+	+
Amaranthus dubius	+	+	-	-	-	-
Amaranthus lividus	+	+	+	+	+	-
Amaranthus patulus	+	+	+	-	+	-
Amaranthus spinosus	+	+	+	+	+	-
Amaranthus viridis	+	+	+	+	+	+
Ambrosia artemisiifolia	+	+	+	+	+	-
Ammannia auriculata	-	+	+	+	+	+
Ammannia coccinea	-	+	+	+	+	+

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Species	VPRD	VPAG	SPT	B	RT	U
Anredera cordifolia	+	+	+	+	+	+
Arachis hypogaea	-	+	-	-	-	-
Ardisia squamulosa	+	+	+	+	+	+
Argemone mexicana	-	+	+	+	+	+
Asclepias curassavica	+	-	+	+	+	+
Asparagus densiflorus var. *sprengeri*	+	+	+	+	-	-
Aster subulatus	+	+	+	+	+	+
Aster subulatus var. *sandwicensis*	+	+	+	+	+	+
Asystasia gangetica subsp. *micrantha*	-	+	+	+	+	-
Austroeupatorium inulifolium	+	-	+	+	+	-
Avena sativa	-	-	+	+	+	+
Axonopus affinis	+	+	+	+	+	+
Axonopus compressus	+	+	+	+	+	+
Azolla mexicana	-	+	+	-	+	-
Bambusa stenostachya	-	-	+	-	-	-
Basella alba	+	+	+	+	+	+
Belamcanda chinensis	+	+	+	+	+	+
Bellis perennis	-	-	+	+	-	-
Bidens alba var. *radiata*	+	+	+	+	+	-
Bidens bipinnata	+	+	+	+	+	-
Bidens pilosa	+	+	+	+	+	-
Blechum pyramidatum	+	-	+	+	+	-
Boehmeria nivea var. *nivea*	+	+	+	+	+	+
Boerhavia coccinea	+	+	+	+	+	-
Boerhavia erecta	+	-	+	+	+	-
Bombax malabaricum	-	-	+	+	+	+
Brachiaria mutica	+	+	+	+	+	+
Bromus catharticus	+	+	+	+	+	+
Brugmansia suaveolens	+	+	+	+	+	+

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Species	VPRD	VPAG	SPT	B	RT	U
Bryophyllum pinnatum	+	+	-	-	-	-
Cajanus cajan	-	+	+	+	+	+
Callisia repens	+	-	+	+	+	+
Callitriche peploides	-	-	+	+	+	-
Calopogonium mucunoides	+	+	+	+	+	+
Calyptocarpus vialis	+	+	+	+	+	+
Canna edulis	+	-	-	-	-	-
Canna indica	+	+	+	+	-	-
Capsella bursa-pastoris	+	+	+	+	+	-
Capsicum annuum	-	-	+	+	+	+
Cardamine flexuosa	+	+	+	+	+	-
Cardiospermum halicacabum	+	+	+	+	+	+
Catharanthus roseus	+	+	+	+	+	+
Celosia argentea	+	+	+	+	+	+
Cenchrus echinatus	+	+	+	+	+	-
Centrosema pubescens	+	+	+	+	+	+
Chamaecrista mimosoides	+	+	+	+	+	-
Chamaecrista nictitans var. *glabrata*	+	+	+	+	-	-
Chenopodium ambrosioides	+	+	+	+	+	+
Chloris barbata	+	+	+	+	+	+
Chloris divaricata var. *cynodontoides*	+	+	+	+	+	-
Chloris gayana	+	+	+	+	+	-
Chloris virgata	+	+	+	+	+	+
Chromolaena odorata	+	+	+	+	+	+
Cinnamomum burmannii	-	+	+	+	+	-
Cissus sicyoides	-	+	+	+	+	+
Cleome rutidosperma	+	+	+	+	+	+
Clerodendrum chinense	+	-	+	+	+	+
Clitoria falcata	-	-	+	+	+	-

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Species	VPRD	VPAG	SPT	B	RT	U
Clitoria ternatea	+	+	+	+	+	+
Coccinia grandis	+	+	+	+	+	-
Coix lacryma-jobi	+	-	+	+	+	+
Coleus amboinicus	+	+	+	+	-	-
Colocasia esculenta	+	+	+	+	+	+
Conyza bonariensis	+	+	+	+	+	-
Conyza canadensis var. *canadensis*	+	+	+	+	+	+
Conyza canadensis var. *pusilla*	+	+	-	-	-	-
Conyza sumatrensis	+	+	+	+	+	+
Corchorus capsularis	+	+	+	+	+	+
Corchorus olitorius	+	+	+	+	+	+
Coreopsis tinctoria	+	+	+	+	+	+
Coronopus didymus	+	+	+	+	+	-
Cosmos bipinnatus	+	+	+	+	+	+
Crassocephalum crepidioides	+	+	+	+	+	+
Crocosmia × *crocosmiiflora*	+	-	-	-	-	-
Crotalaria incana	-	+	+	+	+	+
Crotalaria micans	+	+	+	+	+	+
Crotalaria pallida var. *obovata*	+	+	+	+	+	+
Crotalaria spectabilis	-	+	+	+	+	+
Crotalaria zanzibarica	+	+	+	+	+	+
Croton bonplandianus	-	-	+	+	+	-
Cuphea carthagenensis	+	+	+	+	+	+
Cuscuta campestris	+	+	+	+	+	-
Cuscuta japonica var. *japonica*	+	-	+	+	+	-
Cyclospermum leptophyllum	+	+	+	+	+	-
Cymbopogon nardus	-	-	+	+	+	+
Cynodon nlemfuensis	+	+	+	+	+	-
Cyperus alternifolius	-	+	+	+	+	+

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Species	VPRD	VPAG	SPT	B	RT	U
Cyperus difformis	+	+	+	+	+	+
Cyperus eragrostis	+	+	+	+	+	+
Cyperus esculentus	-	+	+	+	+	+
Cyperus involucratus	+	+	-	-	-	-
Cyperus surinamensis	-	-	+	+	+	+
Cyphomandra betacea	+	-	+	+	+	+
Dactylis glomerata	+	-	+	+	+	+
Delonix regia	-	-	+	+	+	+
Dendrocalamus latiflorus	+	-	+	+	+	-
Derris elliptica	+	+	+	+	+	-
Desmanthus virgatus	-	-	+	+	+	-
Desmodium scorpiurus	+	+	+	+	+	-
Desmodium tortuosum	+	+	+	+	+	-
Desmodium uncinatum	+	-	+	+	+	+
Dichanthium annulatum	+	+	+	+	+	-
Digitalis purpurea	+	+	+	+	+	+
Digitaria sanguinalis	+	+	+	+	+	-
Dioscorea alata	-	+	+	+	-	-
Drymaria diandra	+	+	+	+	+	+
Duchesnea indica	+	+	+	+	+	+
Duranta repens	+	-	+	+	+	+
Eclipta zippeliana	+	-	+	-	+	-
Egeria densa	-	+	+	+	+	+
Eichhornia crassipes	-	-	+	+	+	+
Elephantopus mollis	+	+	+	+	+	+
Emilia fosbergii	+	+	+	+	+	+
Emilia praetermissa	+	+	+	+	+	+
Eragrostis ciliaris	+	+	+	+	+	-
Eragrostis curvula	-	-	+	+	+	+

Species	VPRD	VPAG	SPT	B	RT	U
Erechtites hieracifolia	+	+	+	+	+	+
Erechtites valerianifolia	+	+	+	+	+	-
Erigeron annuus	+	+	+	+	+	-
Erodium moschatum	+	-	+	+	+	-
Euphorbia cyathophora	+	+	+	+	+	+
Euphorbia graminea	-	+	+	+	+	-
Euphorbia heterophylla	+	+	+	+	+	+
Euphorbia hirta	+	+	+	+	+	+
Euphorbia hypericifolia	+	+	+	+	+	-
Euphorbia hyssopifolia	+	+	+	+	+	-
Euphorbia maculata	+	-	+	+	+	-
Euphorbia serpens	+	+	+	+	+	-
Euphoria longana	+	+	-	-	-	-
Eutrema japonicum	-	-	+	+	+	+
Festuca arundinacea	+	+	+	+	+	+
Ficus religiosa	+	-	+	+	+	+
Flueggea suffruticosa	+	+	+	+	+	+
Foeniculum vulgare	+	+	+	+	+	+
Gaillardia pulchella	-	-	+	+	+	+
Galinsoga parviflora	+	+	+	+	+	-
Galinsoga quadriradiata	+	+	+	+	+	-
Geranium carolinianum	+	+	+	+	+	+
Gladiolus gandavensis	+	-	-	-	-	-
Glycine max	-	+	+	+	+	+
Gnaphalium calviceps	+	+	+	-	+	-
Gnaphalium pensylvanicum	+	+	+	+	+	+
Gnaphalium purpureum	+	+	+	+	+	+
Gnaphalium spicatum	+	+	+	+	+	-
Gomphrena celosioides	+	+	+	+	+	+

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Species	VPRD	VPAG	SPT	B	RT	U
Gymnocoronis spilanthoides	-	-	+	+	+	-
Gynura bicolor	+	+	+	+	+	+
Hedychium coronarium	+	+	+	+	+	+
Helianthus debilis subsp. *cucumerifolius*	+	+	+	+	+	-
Heliotropium indicum	+	+	+	+	+	+
Heliotropium procumbens var. *depressum*	+	+	+	-	+	-
Hemerocallis fulva	+	-	+	+	+	+
Holcus lanatus	+	+	+	+	+	-
Hordeum vulgare	-	+	+	+	-	+
Hydrocotyle leucocephala	+	+	+	+	+	+
Hylocereus undatus	+	+	+	+	+	+
Hypochaeris radicata	+	+	+	+	+	-
Hyptis rhomboidea	+	+	-	-	-	-
Hyptis suaveolens	+	+	+	+	+	+
Impatiens balsamina	+	+	+	+	-	-
Ipomoea aquatica	+	+	+	+	-	+
Ipomoea batatas	+	+	+	+	+	+
Ipomoea cairica	+	+	+	+	+	+
Ipomoea eriocarpa	-	+	+	+	+	-
Ipomoea hederacea	+	+	+	+	+	+
Ipomoea hederifolia	-	+	+	+	+	-
Ipomoea indica	+	+	+	+	+	+
Ipomoea nil	+	+	+	+	+	+
Ipomoea obscura	+	+	+	+	+	+
Ipomoea purpurea	-	+	+	+	+	+
Ipomoea quamoclit	+	+	+	+	+	+
Ipomoea triloba	+	+	+	+	+	+
Ipomoea wrightii	-	-	+	+	+	-
Jacquemontia tamnifolia	-	-	+	+	+	-

Species	VPRD	VPAG	SPT	B	RT	U
Justicia gendarussa	-	+	+	+	+	-
Kalanchoe delagoensis	+	-	-	-	-	-
Kyllinga polyphylla	-	-	+	+	+	+
Lablab purpureus	+	+	+	+	+	+
Lantana camara	+	+	+	+	+	+
Laportea aestuans	+	-	+	+	+	-
Leersia hexandra	+	+	+	+	+	-
Lepidium bonariense	+	+	+	+	+	-
Lepidium virginicum	+	+	+	+	+	-
Leptochloa fusca subsp. *uninervia*	-	+	+	+	+	-
Leucaena leucocephala	+	+	+	+	+	+
Leucanthemum vulgare	-	-	+	+	+	+
Lindernia dubia var. *anagallidea*	-	+	-	-	-	-
Lindernia dubia var. *dubia*	-	+	+	+	+	-
Lolium multiflorum	+	+	+	+	+	+
Lolium perenne	+	+	+	+	+	-
Ludwigia decurrens	+	+	+	+	+	-
Ludwigia erecta	+	+	+	+	+	+
Lycium chinense	+	-	+	+	+	+
Lycopersicon esculentum var. *cerasiforme*	+	+	-	-	-	-
Lysimachia candida	+	+	+	+	+	+
Macroptilium atropurpureum	+	+	+	+	+	+
Macroptilium lathyroides	+	+	+	+	+	+
Malva cathayensis	+	-	-	-	-	-
Malva neglecta	+	+	+	+	+	+
Malvastrum coromandelianum	+	+	+	+	+	-
Malvastrum spicatum	+	+	+	+	+	-
Manihot esculenta	+	+	+	+	+	+
Mecardonia procumbens	+	+	+	+	+	-

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Species	VPRD	VPAG	SPT	B	RT	U
Medicago lupulina	+	+	+	+	+	+
Medicago polymorpha	+	+	+	+	+	+
Megathyrsus maximus	+	+	+	+	+	+
Melilotus indicus	+	+	+	+	+	-
Melilotus officinalis	-	+	+	+	+	+
Melinis repens	+	+	+	+	+	+
Melothria pendula	+	+	+	+	+	-
Mentha canadensis	-	-	+	+	-	-
Mikania micrantha	+	+	+	+	+	+
Mimosa diplotricha	+	+	+	+	+	-
Mimosa pigra	+	+	+	+	+	+
Mimosa pudica	+	+	+	+	+	+
Mirabilis jalapa	+	+	+	+	+	+
Mollugo verticillata	-	-	+	+	+	+
Momordica charantia	+	+	+	+	+	+
Momordica charantia var. *abbreviata*	+	+	+	+	+	-
Monochoria vaginalis	+	+	+	+	+	+
Muntingia calabura	+	+	+	+	+	+
Myosotis arvensis	+	-	+	+	+	-
Nasturtium officinale	+	+	+	+	+	+
Neonotonia wightii	+	+	+	+	+	+
Nicandra physalodes	-	+	+	+	+	+
Nicotiana longiflora	-	-	+	+	+	+
Nicotiana plumbaginifolia	+	+	+	+	+	-
Nicotiana tabacum	+	+	+	+	+	+
Ocimum basilicum	+	+	+	+	+	+
Ocimum gratissimum	+	+	+	+	+	+
Ocimum sanctum	+	-	+	+	+	+
Oenothera biennis	+	-	+	+	+	+

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Species	VPRD	VPAG	SPT	B	RT	U
Oenothera laciniata	+	+	+	+	+	-
Oenothera stricta	+	-	+	+	+	-
Opuntia dillenii	-	-	+	+	+	+
Oxalis corymbosa	+	+	-	-	-	-
Pachira macrocarpa	+	+	+	+	+	+
Pachyrhizus erosus	-	-	+	+	-	-
Panicum miliaceum	-	+	+	+	+	+
Panicum repens	+	+	+	+	+	+
Parthenium hysterophorus	+	+	+	+	+	+
Paspalidium flavidum	+	+	+	+	+	-
Paspalum conjugatum	+	+	+	+	+	+
Paspalum dilatatum	+	+	+	+	+	+
Paspalum notatum	+	+	+	+	+	+
Paspalum paniculatum	+	+	+	+	+	-
Paspalum urvillei	+	+	+	+	+	-
Paspalum virgatum	-	+	-	-	-	-
Passiflora edulis	+	+	+	+	+	+
Passiflora foetida var. *hispida*	+	+	+	+	+	+
Passiflora suberosa	+	+	+	+	+	+
Pennisetum polystachion	+	+	+	+	+	-
Pennisetum purpureum	+	+	+	+	+	+
Peperomia pellucida	+	-	+	+	+	+
Perilla frutescens	+	+	+	+	+	+
Persicaria capitata	-	-	+	+	+	+
Phyla nodiflora	+	+	+	+	-	-
Phyllanthus amarus	+	+	+	+	+	-
Phyllanthus debilis	+	+	+	+	+	-
Phyllanthus tenellus	+	+	+	+	+	-
Phyllostachys pubescens	-	-	+	+	+	+

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Species	VPRD	VPAG	SPT	B	RT	U
Physalis angulata	+	+	+	+	+	+
Physalis minima	-	+	-	-	-	-
Physalis peruviana	+	+	+	+	+	+
Physalis pubescens	+	+	+	+	+	+
Phytolacca americana	+	+	+	+	+	+
Pilea microphylla	+	+	+	+	+	+
Piper betle	+	+	+	+	+	+
Pistia stratiotes	+	+	+	+	+	+
Pityrogramma calomelanos	+	+	+	+	+	-
Plantago lanceolata	+	-	+	+	+	-
Plantago virginica	+	-	+	+	+	-
Pluchea carolinensis	+	+	+	+	+	-
Pluchea sagittalis	+	+	+	+	+	-
Plumbago zeylanica	+	-	+	+	+	+
Poa trivialis	+	-	+	+	+	-
Polygala paniculata	+	-	+	+	+	-
Polygonum plebeium	+	+	+	+	-	+
Polypogon monspeliensis	+	+	+	+	+	-
Portulaca pilosa subsp. *grandiflora*	+	-	-	-	-	-
Potentilla amurensis	-	+	-	-	-	-
Praxelis clematidea	+	+	+	+	+	-
Pseudelephantopus spicatus	-	-	+	+	+	-
Pueraria lobata subsp. *thomsonii*	+	+	+	+	+	-
Richardia brasiliensis	+	+	+	+	-	-
Richardia scabra	+	+	+	+	+	+
Ricinus communis	+	+	+	+	+	+
Rivina humilis	+	-	+	+	+	+
Rorippa dubia	+	+	+	+	+	-
Rorippa palustris	-	+	+	+	+	-

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Species	VPRD	VPAG	SPT	B	RT	U
Rotala ramosior	-	-	+	+	+	+
Ruellia brittoniana	+	-	+	+	-	-
Ruellia tuberosa	+	+	+	+	+	-
Rumex acetosella	+	+	+	+	+	+
Rumex crispus var. *crispus*	+	+	+	+	+	+
Rumex crispus var. *japonicus*	+	+	-	-	-	-
Rumex maritimus	-	+	+	+	+	+
Rumex obtusifolius	+	+	+	+	-	+
Salvia coccinea	+	-	+	+	+	-
Schinus terebinthifolia	+	+	+	+	+	-
Scoparia dulcis	+	+	+	+	+	+
Sechium edule	+	-	+	+	+	+
Sedum mexicanum	-	-	+	+	+	+
Selaginella uncinata	-	-	+	+	+	+
Senecio vulgaris	+	+	+	+	+	-
Senna × *floribunda*	+	-	-	-	-	-
Senna alata	+	-	+	+	+	+
Senna occidentalis	+	+	+	+	+	-
Senna sulfurea	+	-	+	+	+	+
Senna tora	-	+	-	-	-	-
Sesbania cannabina	+	+	+	+	-	-
Sesbania sesban	+	+	+	+	+	+
Setaria geniculata	+	+	-	-	-	-
Setaria glauca	+	+	+	-	+	-
Setaria italica	+	-	+	+	+	+
Setaria palmifolia	+	+	+	+	+	+
Setaria sphacelata	+	-	+	+	+	+
Setcreasea purpurea	-	+	+	+	+	+
Sida rhomboidea	+	+	+	+	-	-

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Species	VPRD	VPAG	SPT	B	RT	U
Sisyrinchium atlanticum	+	+	+	+	+	+
Sisyrinchium exile	+	+	+	+	+	-
Sisyrinchium iridifolium	+	-	+	+	+	+
Solanum americanum	+	+	+	+	+	+
Solanum capsicoides	+	+	+	+	+	+
Solanum diphyllum	+	+	+	+	+	+
Solanum erianthum	+	+	+	+	+	+
Solanum melongena	-	-	+	+	+	+
Solanum pseudocapsicum	+	+	+	+	+	+
Solanum sisymbriifolium	+	+	+	+	+	-
Solanum torvum	+	+	+	+	+	+
Solanum tuberosum	+	+	+	+	+	+
Soliva anthemifolia	+	+	+	+	+	+
Soliva pterosperma	+	-	+	+	+	-
Sonchus arvensis	+	+	+	+	+	+
Sonchus asper	+	+	+	+	+	-
Sonchus oleraceus	+	+	+	+	+	+
Sorghum bicolor subsp. *bicolor*	+	+	+	+	+	+
Sorghum halepense	+	+	+	+	+	+
Spathodea campanulata	+	+	+	+	+	+
Spergula arvensis	-	+	+	+	+	+
Spermacoce articularis	+	+	+	+	+	-
Spermacoce assurgens	+	+	+	+	+	-
Spermacoce latifolia	+	+	+	+	+	-
Spermacoce mauritiana	+	+	+	+	+	-
Stachys arvensis	+	-	+	+	+	-
Stachytarpheta cayennensis	+	+	+	+	+	+
Stachytarpheta jamaicensis	+	+	+	+	+	+
Stachytarpheta urticaefolia	+	+	+	-	+	+

Species	VPRD	VPAG	SPT	B	RT	U
Stellaria media	+	+	+	+	+	+
Stemodia verticillata	-	-	+	+	+	-
Stenotaphrum secundatum	-	-	+	+	+	+
Striga lutea	-	-	+	+	+	-
Strobilanthes cusia	+	+	+	+	+	-
Swietenia mahagoni	-	-	+	+	+	+
Symphytum officinale	-	-	+	+	+	+
Synedrella nodiflora	+	+	+	+	+	+
Syngonium podophyllum	+	+	+	+	+	+
Talinum paniculatum	+	+	+	+	+	+
Taraxacum officinale	+	-	+	+	+	+
Tectona grandis	+	-	+	+	+	-
Tephrosia candida	-	-	+	+	+	+
Thunbergia alata	+	+	+	+	+	+
Thunbergia grandiflora	+	-	+	+	+	+
Tithonia diversifolia	+	+	+	+	+	+
Tradescantia fluminensis	+	+	+	+	+	+
Triadica sebifera	+	+	+	+	+	+
Trianthema portulacastrum	+	+	-	-	-	-
Tridax procumbens	+	+	+	+	+	+
Trifolium dubium	+	+	+	+	+	+
Trifolium repens	+	+	+	+	+	+
Triticum aestivum	+	-	+	+	-	-
Verbena bonariensis	+	+	+	+	+	+
Verbena brasiliensis	+	-	+	+	+	+
Vernicia fordii	+	-	+	+	+	+
Vernicia montana	+	+	+	+	+	+
Veronica arvensis	-	-	+	+	+	+
Veronica peregrina	+	+	+	+	+	+

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Species	VPRD	VPAG	SPT	B	RT	U
Veronica persica	+	+	+	+	+	+
Vicia cracca	+	+	+	+	+	-
Vicia hirsuta	-	-	+	+	+	-
Vicia sativa subsp. *nigra*	+	-	+	+	+	-
Vicia tetrasperma	-	+	+	+	+	-
Vigna radiata	+	+	+	+	+	+
Vigna umbellata	+	+	+	+	+	+
Vulpia myuros	+	-	+	+	+	-
Waltheria americana	+	-	+	+	+	+
Wedelia trilobata	+	+	+	+	+	+
Xanthium strumarium	+	+	+	+	+	+
Xanthosoma sagittifolium	+	+	+	+	+	+
Zea mays	-	+	+	+	+	+
Zebrina pendula	+	+	+	+	+	+
Zingiber officinale	+	-	+	+	+	+
Zizania latifolia	-	+	+	+	+	+
Zoysia japonica	-	-	+	+	+	+

+: The species is included in the analysis. -: The species is not included in the analysis. VPRD: Variation partitioning on species in roadside habitat. VPAG: variation partitioning on species in agriculture habitat. SPT: correlation analysis for species preference temperature in their native range and Taiwan. Regression of the temperature deviation on the alien species attributes: major native biome (B), residence time (RT), usage (U).

Appendix 3-1: R code for plot-level analysis

```
#### 1. packages ####
library(readxl)
library(tidyverse)
library(iNEXT)
library(sf)
library(vegan)
#### 2.potential species pool size (PSPS)-RD/AG ####
#### 2-1. select grids and species ####
### select grids
url.splot <- "IM_SPLOTDATA.xlsx" # address from gitHub
tf <-  tempfile(fileext = ".xlsx") # place to save xlsx temporarily
curl::curl_download(url.splot, tf)
SPLOT <- read_xlsx(tf)
# the plot size is 1 by 10 m square (4)
# in mainland
# 01 (roadside), 03, 04, 05 (agriculture)
SPLOT <- SPLOT %>% filter(., SUB_TYPE == 4, MAIN_OFF == 0, HAB_TYPE %in%
c("01", "03", "04", "05"))
# pick up the gird with plot number more than 2
PLOT_grid <- aggregate(SPLOT$SUB_ID ~ SPLOT$PLOT_ID, FUN = function(x)
length(x))
grid_name <- PLOT_grid[PLOT_grid[,2] > 2, 1]
SPLOT <- SPLOT[SPLOT$PLOT_ID %in% grid_name, ]
SPLOT$PLOT_ID_CO <- apply(SPLOT[,1:3], 1, FUN = function(x) paste(x,
collapse = "|"))


### PLOT ID of two habitat types
PLOT_ID_01 <- SPLOT$PLOT_ID[SPLOT$HAB_TYPE == "01"] %>% unique()
PLOT_ID_AG <- SPLOT$PLOT_ID[SPLOT$HAB_TYPE %in% c("03","04","05")] %>%
unique()


### Calculate mean elevation per grid
ELE <- aggregate(ALTT ~ PLOT_ID, data = SPLOT, FUN = function (x)
mean(as.numeric(x)))


### select species by habitat
```

```
url.bio <- " IM(Bio%20data)_noWC.xlsx"
tf <- tempfile(fileext = ".xlsx")
curl::curl_download(url.bio, tf)
BIO <- read_xlsx(tf)

url.name <- " Namebase_total_sp.xlsx"
tf <- tempfile(fileext = ".xlsx")
curl::curl_download(url.name, tf)
NAME <- read_xlsx(tf)
BIO <- BIO %>% filter(PLOT_ID_CO %in% SPLOT$PLOT_ID_CO) %>%
  select(PLOT_ID_CO, ALTT, code) %>% left_join(.,NAME[,
c("chname","code","naturalized","cultivated","latinname")], by = "code")
BIO$PLOT_ID <- substr(BIO$PLOT_ID_CO, start = 1, stop = 6)
BIO$HAB_TYPE <- substr(BIO$PLOT_ID_CO, start = 8, stop = 9)
BIO$SUB_ID <- substr(BIO$PLOT_ID_CO, start = 11, stop = 12)

### Split BIO by habitat type
BIO_01 <- BIO[BIO$HAB_TYPE == "01" & BIO$naturalized == 1 &
BIO$cultivated != 1,]
BIO_AG <- BIO[BIO$HAB_TYPE %in% c("03","04","05") & BIO$naturalized == 1 &
BIO$cultivated != 1,]

### collect species names (remove author's names)
library(flora)
rm.author <- function(sp){
  sp <- sapply(sp, function(x) remove.authors(x))
  sp[sp == "Portulaca pilosa grandiflora"] <- "Portulaca pilosa ssp.
grandiflora"
  sp[sp == "Chamaecrista nictitans var. glabrata"] <- "Chamaecrista
nictitans ssp. patellaria var. glabrata"
  sp[sp == "Vicia sativa nigra"] <- "Vicia sativa ssp. nigra"
  sp[sp == "Spermacoce articularis f."] <- "Spermacoce articularis"
  sp[sp == "Tectona grandis f."] <- "Tectona grandis"
  sp[sp == "Justicia gendarussa f."] <- "Justicia gendarussa"
  sp[sp == "Asystasia gangetica micrantha"] <- "Asystasia gangetica ssp.
micrantha"
  sp[sp == "Acmella paniculata Jansen"] <- "Acmella paniculata"
  sp[sp == "Helianthus debilis"] <- "Helianthus debilis ssp.
cucumerifolius"
```

```
  sp[sp == "Leptochloa fusca uninervia"] <- "Leptochloa fusca spp.
uninervia"
  return(sp)
}

Name_01 <- rm.author(unique(BIO_01$latinname))
Name_AG <- rm.author(unique(BIO_AG$latinname))

#### 2-2. Calculation PSPS and join Temperature and Land-use ####
### import species temp data
NAT.gbif <- read.csv("IM_GBIF_NAT_WC_Tavg_complete(no%20TW).csv")
# temperature from occurrence
NAT.gbif <- NAT.gbif[!is.na(NAT.gbif$mean),]
NAT.POWO <- read.csv("IM_POWO_NAT_WC_Tavg_plus%20occ-
deficiency%20species(updated).csv")
# temp from mean of native countries
# merge two sources, if one species occurs in both GBIF and POWO, use GBIF
in priority
NAT <- rbind (NAT.gbif,
              NAT.POWO [!(NAT.POWO$species %in% NAT.gbif$species),])
df <- NAT[,c("species","mean","no_of_record","sd","min","max")]
%>% .[complete.cases(.),]
df_01 <- df[df$species %in% Name_01,]
df_AG <- df[df$species %in% Name_AG,]

### Grid temp
url.grid.temp <- plot%20centroid_climate.shp"
grid_temp <- st_read(url.grid.temp) %>%
  select(PLOT_ID, tavg) %>% st_drop_geometry()
grid_temp$PLOT_ID <- as.character(grid_temp$PLOT_ID)

### potential species pool size
grid_temp$SpPool_01 <- sapply(grid_temp$tavg, FUN = function(x) {
  sum(apply(df_01, 1, FUN = function(y) {
         Mean = as.numeric (y[2])
         Sd = as.numeric (y[4])
         out <- x >= Mean-Sd & x <= Mean+Sd
         return(out)} ))
```

```
  })
grid_temp$SpPool_AG <- sapply(grid_temp$tavg, FUN = function(x) {
  sum(apply(df_AG, 1, FUN = function(y) {
    Mean = as.numeric (y[2])
    Sd = as.numeric (y[4])
    out <- x >= Mean-Sd & x <= Mean+Sd
    return(out)} ))
})

### import Land use
load(url("buf2k_1k_LU_sprd.Rdata"))
buf2k_1k_LU_sprd$PLOT_ID <- as.character(buf2k_1k_LU_sprd$PLOT_ID)

### import road length
road.length <- read.csv("road%20length_2k_1k.csv")

### import standardized species richness
load(url("est_ntr01_update.Rdata"))
load(url("est_ntrAG_update.Rdata"))
est_ntr01$PLOT_ID <- rownames(est_ntr01)
est_ntrAG$PLOT_ID <- rownames(est_ntrAG)
est_ntr01 <- SPLOT %>% filter(PLOT_ID %in% est_ntr01$PLOT_ID, HAB_TYPE ==
"01") %>%
  group_by(PLOT_ID) %>% summarise(Elevation = mean(as.numeric(ALTT))) %>%
  left_join(est_ntr01,. ,by = "PLOT_ID")
est_ntrAG <- SPLOT %>%
  filter(PLOT_ID %in% est_ntrAG$PLOT_ID, HAB_TYPE %in% c("03","04","05"))
%>%
  group_by(PLOT_ID) %>% summarise(Elevation = mean(as.numeric(ALTT))) %>%
  left_join(est_ntrAG,. ,by = "PLOT_ID")

### joint elevation & land use & road length & species richness
Vp_df_01 <- merge(grid_temp, ELE[ELE$PLOT_ID %in% PLOT_ID_01,]) %>%
  merge(., buf2k_1k_LU_sprd[, c("PLOT_ID","01","03")]) %>%
  merge(., road.length[,c("PLOT_ID", "ring_road_length")]) %>%
  merge(., est_ntr01[,c("PLOT_ID","q = 0")])
```

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```
Vp_df_01 <- Vp_df_01[,c("PLOT_ID", "q = 0",
"ALTT","tavg","SpPool_01","01","03","ring_road_length")]
%>% .[complete.cases(.),]

Vp_df_AG <- merge(grid_temp, ELE[ELE$PLOT_ID %in% PLOT_ID_AG,]) %>%

  merge(., buf2k_1k_LU_sprd[, c("PLOT_ID","01","03")]) %>%

  merge(., road.length[,c("PLOT_ID", "ring_road_length")]) %>%

  merge(., est_ntrAG[,c("PLOT_ID","q = 0")])

Vp_df_AG <- Vp_df_AG[,c("PLOT_ID","ALTT", "q = 0",
"tavg","SpPool_AG","01","03","ring_road_length")] %>% .[complete.cases(.),]


####  3. variation partitioning (Road, AG) ####

library(vegan)

VP_01 <- varpart(sqrt(Vp_df_01$`q = 0`), ~SpPool_01,
~sqrt(`01`)+sqrt(`ring_road_length`), data = Vp_df_01)

VP_AG <- varpart(sqrt(Vp_df_AG$`q = 0`), ~SpPool_AG,
~sqrt(`01`)+sqrt(`ring_road_length`), data = Vp_df_AG)

windows()

par(mfrow = c(1,2))

plot(VP_01, Xnames = c("STP", "HA")); title(main = "Roadside habitat")

plot(VP_AG, Xnames = c("STP", "HA")); title(main = "Agricultural habitat")


#### 4-1. Test each segment - Roadside ####

lm_all.01 <- lm (scale(sqrt(`q = 0`)) ~ scale(SpPool_01) +
scale(sqrt(`01`)) + scale(sqrt(`ring_road_length`)), data = Vp_df_01)

summary (lm_all.01)

vif(lm_all.01)


# test partial effect

lm_SPT.01 <- lm (scale(sqrt(`q = 0`)) ~ scale(SpPool_01), data = Vp_df_01)

lm_HA.01 <- lm (scale(sqrt(`q = 0`)) ~ scale(sqrt(`01`)) +
scale(sqrt(ring_road_length)), data = Vp_df_01)

summary(lm_SPT.01)

summary(lm_HA.01)

anova(lm_SPT.01, lm_all.01)

anova(lm_HA.01, lm_all.01)




#### 4-2. Test each segment - AG ####
```

```
lm_all.AG <- lm (scale(sqrt(`q = 0`)) ~ scale(SpPool_AG) +
scale(sqrt(`01`)) + scale(sqrt(ring_road_length)), data = Vp_df_AG)
summary (lm_all.AG)
vif(lm_all.AG)

### test partial effect
lm_SPT.AG <- lm (scale(sqrt(`q = 0`)) ~ scale(SpPool_AG), data = Vp_df_AG)
lm_HA.AG <- lm (scale(sqrt(`q = 0`)) ~ scale(sqrt(`01`)) +
scale(sqrt(ring_road_length)), data = Vp_df_AG)
summary(lm_SPT.AG)
summary(lm_HA.AG)
anova(lm_SPT.AG, lm_all.AG)
anova(lm_HA.AG, lm_all.AG)

#### 5. Potential species pool size-Trop/Temp, RD/AG ####
### import species richness (group by climatic orgin)
load(url("est_trop01.Rdata"))
load(url("est_tropAG.Rdata"))
load(url("est_temp01.Rdata"))
load(url("est_tempAG.Rdata"))
est_temp01$PLOT_ID <- rownames(est_temp01)
est_tempAG$PLOT_ID <- rownames(est_tempAG)
est_trop01$PLOT_ID <- rownames(est_trop01)
est_tropAG$PLOT_ID <- rownames(est_tropAG)

### select species by habitat and bioclimatic origin
load(url("BIO.temp.01.Rdata"))
load(url("BIO.trop.01.Rdata"))
load(url("BIO.temp.AG.Rdata"))
load(url("BIO.trop.AG.Rdata"))

Name_trop01 <- unique(BIO.trop.01$species)
Name_tropAG <- unique(BIO.trop.AG$species)
Name_temp01 <- unique(BIO.temp.01$species)
Name_tempAG <- unique(BIO.temp.AG$species)

df_trop01 <- df[df$species %in% Name_trop01,]
```

```
df_tropAG <- df[df$species %in% Name_tropAG,]
df_temp01 <- df[df$species %in% Name_temp01,]
df_tempAG <- df[df$species %in% Name_tempAG,]

### potential species pool size
grid_temp$SpPool_trop01 <- sapply(grid_temp$tavg, FUN = function(x) {
  sum(apply(df_trop01, 1, FUN = function(y) {
    Mean = as.numeric (y[2])
    Sd = as.numeric (y[4])
    out <- x >= Mean-Sd & x <= Mean+Sd
    return(out)} ))
})
grid_temp$SpPool_tropAG <- sapply(grid_temp$tavg, FUN = function(x) {
  sum(apply(df_tropAG, 1, FUN = function(y) {
    Mean = as.numeric (y[2])
    Sd = as.numeric (y[4])
    out <- x >= Mean-Sd & x <= Mean+Sd
    return(out)} ))
})
grid_temp$SpPool_temp01 <- sapply(grid_temp$tavg, FUN = function(x) {
  sum(apply(df_temp01, 1, FUN = function(y) {
    Mean = as.numeric (y[2])
    Sd = as.numeric (y[4])
    out <- x >= Mean-Sd & x <= Mean+Sd
    return(out)} ))
})
grid_temp$SpPool_tempAG <- sapply(grid_temp$tavg, FUN = function(x) {
  sum(apply(df_tempAG, 1, FUN = function(y) {
    Mean = as.numeric (y[2])
    Sd = as.numeric (y[4])
    out <- x >= Mean-Sd & x <= Mean+Sd
    return(out)} ))
})

### joint elevation & land use & species richness
```

```
Vp_df_trop01 <- merge(grid_temp, ELE[ELE$PLOT_ID %in%
BIO.trop.01$PLOT_ID,]) %>%
  merge(., buf2k_1k_LU_sprd[, c("PLOT_ID","01","03")]) %>%
  merge(., road.length[,c("PLOT_ID","ring_road_length")]) %>%
  merge(., est_trop01[,c("PLOT_ID","q = 0")])
Vp_df_trop01 <- Vp_df_trop01[,c("PLOT_ID", "q = 0",
"ALTT","tavg","SpPool_trop01","01","03", "ring_road_length")]
%>% .[complete.cases(.),]


Vp_df_tropAG <- merge(grid_temp, ELE[ELE$PLOT_ID %in%
BIO.trop.AG$PLOT_ID,]) %>%
  merge(., buf2k_1k_LU_sprd[, c("PLOT_ID","01","03")]) %>%
  merge(., road.length[,c("PLOT_ID","ring_road_length")]) %>%
  merge(., est_tropAG[,c("PLOT_ID","q = 0")])
Vp_df_tropAG <- Vp_df_tropAG[,c("PLOT_ID", "q = 0",
"ALTT","tavg","SpPool_tropAG","01","03", "ring_road_length")]
%>% .[complete.cases(.),]


Vp_df_temp01 <- merge(grid_temp, ELE[ELE$PLOT_ID %in%
BIO.temp.01$PLOT_ID,]) %>%
  merge(., buf2k_1k_LU_sprd[, c("PLOT_ID","01","03")]) %>%
  merge(., road.length[,c("PLOT_ID","ring_road_length")]) %>%
  merge(., est_temp01[,c("PLOT_ID","q = 0")])
Vp_df_temp01 <- Vp_df_temp01[,c("PLOT_ID", "q = 0",
"ALTT","tavg","SpPool_temp01","01","03","ring_road_length")]
%>% .[complete.cases(.),]


Vp_df_tempAG <- merge(grid_temp, ELE[ELE$PLOT_ID %in%
BIO.temp.AG$PLOT_ID,]) %>%
  merge(., buf2k_1k_LU_sprd[, c("PLOT_ID","01","03")]) %>%
  merge(., road.length[,c("PLOT_ID","ring_road_length")]) %>%
  merge(., est_tempAG[,c("PLOT_ID","q = 0")])
Vp_df_tempAG <- Vp_df_tempAG[,c("PLOT_ID", "q = 0",
"ALTT","tavg","SpPool_tempAG","01","03","ring_road_length")]
%>% .[complete.cases(.),]



#### 6. Plots-PSPS vs. MAT & ELE ####
# compare with standardized species richness in each plot
windows()
par(mfrow = c(2,3), cex.lab = 1.5, mgp = c(2.7,1,0))
```

```
plot(Vp_df_01$ALTT, Vp_df_01$SpPool_01,
     xlab = "Elevation (m a.s.l.)", ylab = "Number of species", pch = 20,
     col = "grey", las = 1, cex = 0.7, xlim = c(0,3500), ylim = c(0, 150))
points(Vp_df_01$ALTT, Vp_df_01$`q = 0`, col = "black", pch = 20, cex = 0.7)

plot(Vp_df_trop01$ALTT, Vp_df_trop01$SpPool_trop01,
     xlab = "Elevation (m a.s.l.)", ylab = "Number of species", pch = 20,
     col = "grey", las = 1, cex = 0.7, xlim = c(0,3500), ylim = c(0, 150))
points(Vp_df_trop01$ALTT, Vp_df_trop01$`q = 0`, col = "black", pch = 20,
cex = 0.7)

plot(Vp_df_temp01$ALTT, Vp_df_temp01$SpPool_temp01,
     xlab = "Elevation (m a.s.l.)", ylab = "Number of species", pch = 20,
     col = "grey", las = 1, cex = 0.7, xlim = c(0,3500), ylim = c(0, 150))
points(Vp_df_temp01$ALTT, Vp_df_temp01$`q = 0`, col = "black", pch = 20,
cex = 0.7)

plot(Vp_df_AG$ALTT, Vp_df_AG$SpPool_AG,
     xlab = "Elevation (m a.s.l.)", ylab = "Number of species", pch = 20,
     col = "grey", las = 1, cex = 0.7, xlim = c(0,3500), ylim = c(0, 150))
points(Vp_df_AG$ALTT, Vp_df_AG$`q = 0`, col = "black", pch = 20, cex = 0.7)

plot(Vp_df_tropAG$ALTT, Vp_df_tropAG$SpPool_tropAG,
     xlab = "Elevation (m a.s.l.)", ylab = "Number of species", pch = 20,
     col = "grey", las = 1, cex = 0.7, xlim = c(0,3500), ylim = c(0, 150))
points(Vp_df_tropAG$ALTT, Vp_df_tropAG$`q = 0`, col = "black", pch = 20,
cex = 0.7)

plot(Vp_df_tempAG$ALTT, Vp_df_tempAG$SpPool_tempAG,
     xlab = "Elevation (m a.s.l.)", ylab = "Number of species", pch = 20,
     col = "grey", las = 1, cex = 0.7, xlim = c(0,3500), ylim = c(0, 150))
points(Vp_df_tempAG$ALTT, Vp_df_tempAG$`q = 0`, col = "black", pch = 20,
cex = 0.7)

#### 7. species richness elevation pattern ####
### smooth spline (All hab + RD/AG) ####
windows()
layout(matrix(c(1,1,1,1,2,3), ncol = 3, byrow = F))
```

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```
# All hab
load(url("est_ntr_allHab.Rdata"))
s_spline.01 <- smooth.spline(est_ntr_allHab$ALTT,
                             est_ntr_allHab$`q = 0`,
                             lambda = 0.01)
plot(`q = 0` ~ ALTT, data = est_ntr_allHab, pch = 20, col = "grey", main =
"All habitat types", xlab = "Elevation (m a.s.l.)", ylab = "Standardized
alien species richness", las = 1, cex.lab = 1.2, xlim = c(0,3500), ylim =
c(0,50))
lines(s_spline.01, col = "red", lwd = 2)
title(main = "(a)", font.main = 1, adj = 0, line = 0.5)
# RD
s_spline <- smooth.spline(est_ntr01$Elevation, est_ntr01$`q = 0`, lambda =
0.03)
plot(`q = 0` ~ Elevation, data = est_ntr01, pch = 20, col = "grey", main =
"Roadside habitat", xlab = "Elevation (m a.s.l.)", ylab = "Standardized
alien species richness", las = 1, cex.lab = 1.2,
     xlim = c(0,3500), ylim = c(0,50))
lines(s_spline, col = "red", lwd = 2)
title(main = "(b)", font.main = 1, adj = 0, line = 0.5)
#AG
s_spline_AG <- smooth.spline(est_ntrAG$Elevation, est_ntrAG$`q = 0`, lambda
= 0.05)
plot(`q = 0` ~ Elevation, data = est_ntrAG, pch = 20, col = "grey", main =
"Agricultural habitat", xlab = "Elevation (m a.s.l.)", ylab = "Standardized
alien species richness", las = 1, cex.lab = 1.2,
     xlim = c(0,3500), ylim = c(0,50))
lines(s_spline_AG, col = "red", lwd = 2)
title(main = "(c)", font.main = 1, adj = 0, line = 0.5)


### 8. PSPS in different MAT + 9. species temperature optimal range for
each species ####
sp.pool.01 <- sapply(4:25, FUN = function(x) {
  sum(apply(df_01, 1, FUN = function(y) {
    Mean = as.numeric (y[2])
    Sd = as.numeric (y[4])
    out <- x >= Mean-Sd & x <= Mean+Sd
    return(out)} ))
})
sp.pool.AG <- sapply(4:25, FUN = function(x) {
```

```
  sum(apply(df_AG, 1, FUN = function(y) {
    Mean = as.numeric (y[2])
    Sd = as.numeric (y[4])
    out <- x >= Mean-Sd & x <= Mean+Sd
    return(out)} ))
})
sp.pool.trop01 <- sapply(4:25, FUN = function(x) {
  sum(apply(df_trop01, 1, FUN = function(y) {
    Mean = as.numeric (y[2])
    Sd = as.numeric (y[4])
    out <- x >= Mean-Sd & x <= Mean+Sd
    return(out)} ))
})
sp.pool.tropAG <- sapply(4:25, FUN = function(x) {
  sum(apply(df_tropAG, 1, FUN = function(y) {
    Mean = as.numeric (y[2])
    Sd = as.numeric (y[4])
    out <- x >= Mean-Sd & x <= Mean+Sd
    return(out)} ))
})
sp.pool.temp01 <- sapply(4:25, FUN = function(x) {
  sum(apply(df_temp01, 1, FUN = function(y) {
    Mean = as.numeric (y[2])
    Sd = as.numeric (y[4])
    out <- x >= Mean-Sd & x <= Mean+Sd
    return(out)} ))
})
sp.pool.tempAG <- sapply(4:25, FUN = function(x) {
  sum(apply(df_tempAG, 1, FUN = function(y) {
    Mean = as.numeric (y[2])
    Sd = as.numeric (y[4])
    out <- x >= Mean-Sd & x <= Mean+Sd
    return(out)} ))
})

### 11. species temperature optima range for each species
```

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```
df_order <- df[order(df$mean),]
df_order$opt_max <- df_order$mean+df_order$sd
df_order$opt_min <- df_order$mean-df_order$sd

windows()
par(mfrow = c(1,2), cex.lab = 1.4)
plot(4:25, sp.pool.01, type = "b", pch = 20, xlab = "Mean annual temperature("~degree~"C)", ylab = "Potential species pool size")
points(4:25, sp.pool.AG, col = 2, type = "b", pch = 20)
points(4:25, sp.pool.trop01, col = 3, pch = 20, type = "b")
points(4:25, sp.pool.tropAG, col = 4, pch = 20, type = "b")
points(4:25, sp.pool.temp01, col = 5, pch = 20, type = "b")
points(4:25, sp.pool.tempAG, col = 6, pch = 20, type = "b")
legend("topleft", legend = c("Roadside","Agriculture","Tropical, roadside","Tropical, agriculture", "Temperate, roadside", "Temperate, agriculture"), pch = 19, lty = 1, col = 1:6, bty = "n", cex = 1)
title(main = "(a)",adj = 0, font.main = 1, line = 0.5)
abline(v = 15.40458, lwd = 2)
abline(v = 24.17417, lwd = 2)
# 5%       95%
# 15.40458 24.17417
BP <- barplot(df_order$opt_max, names.arg = "", col = NA, border = NA)
for(i in 1:411){
  arrows(BP[i],df_order$opt_min[i], BP[i], df_order$opt_max[i], angle=90, code=3, length=0.01)
}
box()
# abline(h = 23, lty = 2, col = "red")
title(xlab = "Species",line = 1)
title(ylab = "Temperature ("~degree~"C)", line = 2)
title(main = "(b)",adj = 0, font.main = 1, line = 0.5)

#### 10. elevation v.s human activity ####
cor.01.a <- cor(Vp_df_01$ALTT,Vp_df_01$`01`) %>% round(.,3)
cor.01.l <- cor(Vp_df_01$ALTT,Vp_df_01$ring_road_length) %>% round(.,3)
cor.AG.a <- cor(Vp_df_AG$ALTT,Vp_df_AG$`01`) %>% round(.,3)
cor.AG.l <- cor(Vp_df_AG$ALTT,Vp_df_AG$ring_road_length) %>% round(.,3)
```

```
windows()

par(mfrow = c(2,2))

par(mar = c(5,6,4,2)+0.1)

plot(`01` ~ ALTT, data = Vp_df_01, col = "grey", pch = 20, las = 1, xlab = "Elevation(m a.s.l.)", ylab = "Agriculture area (%)", cex.axis = 0.7)

mtext("(a)", 3, adj = 0, line = 0.5)

mtext("Roadside", 2, line = 4.3, font = 1, cex = 1.7)

legend("topright", legend = bquote("r"==.(cor.01.a)), bty = "n")


plot(ring_road_length/(2000^2*pi-1000^2*pi) ~ ALTT, data = Vp_df_01, col = "grey", pch = 20, las = 1, xlab = "Elevation(m a.s.l.)", ylab = bquote("Road density ("~m/m^2~")"), cex.axis = 0.7)

mtext("(b)", 3, adj = 0, line = 0.5)

legend("topright", legend = bquote("r"==.(cor.01.l)), bty = "n")


plot(`01` ~ ALTT, data = Vp_df_AG, col = "grey", pch = 20, las = 1, xlab = "Elevation(m a.s.l.)", ylab = "Agriculture area (%)", cex.axis = 0.7)

mtext("(c)", 3, adj = 0, line = 0.5)

mtext("Agriculture", 2, line = 4.3, font = 1, cex = 1.7)

legend("topright", legend = bquote("r"==.(cor.AG.a)), bty = "n")


plot(ring_road_length/(2000^2*pi-1000^2*pi) ~ ALTT, data = Vp_df_AG, col = "grey", pch = 20, las = 1, xlab = "Elevation(m a.s.l.)", ylab = bquote("Road density ("~m/m^2~")"), cex.axis = 0.7)

mtext("(d)", 3, adj = 0, line = 0.5)

legend("topright", legend = bquote("r"==.(cor.AG.l)), bty = "n")
```

Appendix 3-2: R code for species-level analysis

```
#### 1. Package ####

library(readxl)

library(tidyverse)

library(vegan)

#### 2. Species preference temperature data frame ####

url.tw <- " IM_TW_WC_Tavg.csv"

url.nat.gbif <- " IM_GBIF_NAT_WC_Tavg_complete(no%20TW).csv"

url.nat.powo <- " IM_POWO_NAT_WC_Tavg_plus%20occ-deficiency%20species(updated).csv"

TW <- read.csv(url.tw) # sp preference temp in TW

NAT.gbif <- read.csv(url.nat.gbif)
```

```
          # temperature from occurrence
NAT.gbif <- NAT.gbif[!is.na(NAT.gbif$mean),]
NAT.POWO <- read.csv(url.nat.powo)
          # temp from mean of native countries
# merge two sources, if one species occurs in both GBIF and POWO, use GBIF
in priority
NAT <- rbind (NAT.gbif,
              NAT.POWO [!(NAT.POWO$species %in% NAT.gbif$species),])
df <- merge(NAT[,c("species","mean","no_of_record","sd","min","max")],
TW[,c("species","mean","no_of_record","sd","min","max")], by = "species")
df$dif <- df$mean.y-df$mean.x
df <- df[complete.cases(df),]

#### 3. Add species attributes ####
url.sp.list <- "20121018-Taiwan%20alien%20species%20list.xlsx"
tf <-  tempfile(fileext = ".xlsx")
curl::curl_download(url.sp.list, tf)
sp.list <- read_xlsx(tf)
source("NameMatch%20function_github.R")
sp.list$species <- name2Taibon(Name.match, sp.list$species)
sp.list$species[sp.list$scientificName == "Chloris divaricata R. Br."] <-
"Chloris divaricata var. divaricata"
sp.list$LF <- sp.list %>% select(Tree,Shrub,Liana,Vine,Herb) %>%
apply(.,1,function(x) names(.)[x == 1])
df.sp <- sp.list %>%
  select(species, specimenYear, publishYear, LF, usage) %>%
  merge(df, .,by = "species", all.x = T) %>%
  filter(no_of_record.x > 2 & no_of_record.y > 2)
df.sp$LF <- factor(df.sp$LF)

#### 3-1 Usage ####
# make "usage column" become dummy variables
for(i in 1:nrow(df.sp)){
  if(grepl("C", df.sp$usage[i])){
    df.sp$Crop[i] <- 1
  }else{
    df.sp$Crop[i] <- 0
  }
```

```
}
for(i in 1:nrow(df.sp)){
  if(grepl("F", df.sp$usage[i])){
    df.sp$Forage[i] <- 1
  }else{
    df.sp$Forage[i] <- 0
  }
}
for(i in 1:nrow(df.sp)){
  if(grepl("M", df.sp$usage[i])){
    df.sp$Medicinal[i] <- 1
  }else{
    df.sp$Medicinal[i] <- 0
  }
}
for(i in 1:nrow(df.sp)){
  if(grepl("O", df.sp$usage[i])){
    df.sp$Ornamental[i] <- 1
  }else{
    df.sp$Ornamental[i] <- 0
  }
}
usage.df <- df.sp[,c("species","Crop","Forage","Medicinal","Ornamental")]
df.sp$Crop <- factor(df.sp$Crop)
df.sp$Forage <- factor(df.sp$Forage)
df.sp$Ornamental <- factor(df.sp$Ornamental)
df.sp$Medicinal <- factor(df.sp$Medicinal)
usage.df <- usage.df[rowSums(usage.df[,-1]) != 0,] # remove no usage
information species


# Ordination to reduce dimensions
DCA.usg <- decorana(usage.df[,-1])
DCA.usg # Axis lengths    3.2491
PCA.usg <- rda(usage.df[,-1])
head(summary(PCA.usg)) # Proportion Explained 0.4765 0.2964 0.1501 (old
result:0.4838 0.2983 0.1397, don't know what cause the difference)
PCA.score.usg <- scores(PCA.usg, display = "sites") %>%
```

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```
  cbind(usage.df$species, .) %>% as.data.frame()
names(PCA.score.usg) <- c("species", "usgPC1", "usgPC2")

df.sp <- merge(df.sp, PCA.score.usg, all.x = T)
df.sp$usgPC1 <- as.numeric(df.sp$usgPC1)
df.sp$usgPC2 <- as.numeric(df.sp$usgPC2)

#### 3-2 residence time ####
# choose older year as the first record year
for(i in 1:nrow(df.sp)){
  if(!is.na(df.sp$specimenYear[i]) | !is.na(df.sp$publishYear[i])){
    df.sp$year[i] <- min(df.sp$specimenYear[i],df.sp$publishYear[i], na.rm = T)
  }else{
    df.sp$year[i] <- NA
  }
}
range(df.sp$year, na.rm = T)
df.sp$year[df.sp$species == "Sida rhomboidea"] <- NA # fix mistype in the data
# residence time = this year - first record year
df.sp$year <- 2022-df.sp$year
# remove the column that will not be used again
df.sp <- df.sp[, setdiff(names(df.sp),c("specimenYear","publishYear"))]
hist(df.sp$year, main = "Histogram of residence time", xlab = "Year", ylab = "Number of species")
box()

#### 3-3 Biome ####
BIOME.df <- read.csv("species%20biome%20matrix_updated.csv", check.names = F)
BIOME.df$species <- name2Taibon(Name.match,BIOME.df$species)
BIOME.df <- BIOME.df[BIOME.df$species %in% df.sp$species,]
setdiff(df.sp$species, BIOME.df$species) # these 8 species do not have biome info

# Major biome in each sp
url.biome.ID <- " BiomeNames.xlsx" # address from gitHub
```

```
tf <-  tempfile(fileext = ".xlsx") # place to save xlsx temporarily
curl::curl_download(url.biome.ID, tf)
ID.df <- read_xlsx(tf) # add biome ID to visualize easily
major.biome <- apply(BIOME.df[,-1], 1, function(x) names(BIOME.df[,-
1])[which.max(x)]) %>% cbind(BIOME.df$species, .) %>% as.data.frame()
names(major.biome) <- c("species","MajorBiome")
major.biome <- merge(major.biome, ID.df, by.x = "MajorBiome", by.y =
"BiomeName")


# Biome.abr <-
c("BorFrst","DsrtXer","FldGr","Lake","Mngr","Mdtr","Mntn","Rock/Ice","TmpBr
dMix","TmpCnf","TmpGrs","TrpCnf","TrpDryBrd","TrpGrs","TrpMisBrd","Tndra")


# merge
df.sp <- merge(df.sp, major.biome, by = "species", all.x = T)
df.sp$TRP_TMP <- ifelse(is.na(df.sp$MajorBiome),"NA",
                        ifelse(grepl(pattern = "Tropical", x =
df.sp$MajorBiome), "TRP",
                         ifelse(grepl(pattern = "Temperate", x =
df.sp$MajorBiome),"TMP","Others")))
df.sp$TRP_TMP <- df.sp$TRP_TMP %>% factor(., levels =
c("TRP","TMP","Others","NA"))
df.sp$BiomeID <- factor(df.sp$BiomeID)


#### 3-3-1 correlation plot with biome colors ####
cor.test(df.sp$mean.x, df.sp$mean.y) # 0.67


bim.col <- c("#df536b","#2297e6","#9e9e9e","#386641")
windows()
par(mar = c(5,5,4,2)+0.1)
plot( mean.y ~ mean.x, data = df.sp, xlim = c(5,30), ylim = c(5,30), type =
"n",
      pch = 20, col = "grey", xlab = bquote("Native range ("~degree~"C)"),
      ylab = bquote("Taiwan ("~degree~"C)"),
      main = "", cex = 1.2, cex.lab = 1.5)
abline(a = 0, b = 1, lty = 2)
abline(a = 3, b = 1, lty = 2, col = "grey")
abline(a = -3, b = 1, lty = 2, col = "grey")
points(mean.y ~ mean.x, data = df.sp, pch = 20, col =
bim.col[as.numeric(df.sp$TRP_TMP)])
```

```
legend("bottomright", c("Tropical","Temperate", "Others", "No
information"),
       pch = 20, title = "Origin",
       col = bim.col) # as.numeric(factor(df.sp$TRP_TMP))
title(main = "(a)", font.main = 1, adj = 0, line = 0.5, cex.main = 2)


# proportion of temperature match / mismatich ####
sum(abs(df.sp$dif) <= 3) # 257 species in 396 species
sum(abs(df.sp$dif) <= 3)/nrow(df.sp) # 0.65


sum(df.sp$dif > 3) # 107 species in 396 species
sum(df.sp$dif > 3)/nrow(df.sp) # 0.27
sum(df.sp$dif < -3) # 32 species in 396 species
sum(df.sp$dif < -3)/nrow(df.sp) # 0.081


# proportion of temperate species ####
sum(abs(df.sp$dif[df.sp$TRP_TMP == "TMP"]) <= 3) # 16 species in 96 species
sum(abs(df.sp$dif[df.sp$TRP_TMP == "TMP"]) <= 3)/sum(df.sp$TRP_TMP ==
"TMP") # 0.167
sum(df.sp$dif[df.sp$TRP_TMP == "TMP"] > 3) # 80 species in 96 species
sum(df.sp$dif[df.sp$TRP_TMP == "TMP"] > 3)/sum(df.sp$TRP_TMP == "TMP") #
0.833
sum(df.sp$dif[df.sp$TRP_TMP == "TMP"] < -3) # 0 species in 96 species


# proportion of tropical species ####
sum(abs(df.sp$dif[df.sp$TRP_TMP == "TRP"]) <= 3) # 223 species in 265
species
sum(abs(df.sp$dif[df.sp$TRP_TMP == "TRP"]) <= 3)/sum(df.sp$TRP_TMP ==
"TRP") # 0.842
sum(df.sp$dif[df.sp$TRP_TMP == "TRP"] > 3) # 12 species in 265 species
sum(df.sp$dif[df.sp$TRP_TMP == "TRP"] > 3)/sum(df.sp$TRP_TMP == "TRP") #
0.045
sum(df.sp$dif[df.sp$TRP_TMP == "TRP"] < -3) # 30 species in 265 species
sum(df.sp$dif[df.sp$TRP_TMP == "TRP"] < -3)/sum(df.sp$TRP_TMP == "TRP") #
0.113


#### 3-3-2 correlation plots with optimum temperature ranges ####
# in Nat
windows(width=14)
```

```
par(mfrow = c(1,2))
par(mar = c(5,5,4,2)+0.1)
plot( mean.y ~ mean.x, data = df.sp, xlim = c(5,30), ylim = c(5,30), las =
1,
      pch = 20, col = bim.col[as.numeric(df.sp$TRP_TMP)], xlab =
bquote("Native range ("~degree~"C)"),
      ylab = bquote("Taiwan ("~degree~"C)"),
      main = "", cex = 1.2, cex.lab = 1.3)
segments(y0 = df.sp$mean.y, y1 = df.sp$mean.y,
         x0 = df.sp$mean.x+df.sp$sd.x,
         x1 = df.sp$mean.x-df.sp$sd.x,
         lwd = 5*df.sp$sd.x/max(df.sp$sd.x),col =
bim.col[as.numeric(df.sp$TRP_TMP)])
legend("bottomright", c("Tropical","Temperate", "Others", "No
information"),
       pch = 20, title = "Origin",
       col = bim.col)
mtext("(a)",3,adj = 0, line = 0.5, cex = 2)
# in TW
plot( mean.y ~ mean.x, data = df.sp, xlim = c(5,30), ylim = c(5,30), las =
1,
      pch = 20, col = bim.col[as.numeric(df.sp$TRP_TMP)], xlab =
bquote("Native range ("~degree~"C)"),
      ylab = bquote("Taiwan ("~degree~"C)"),
      main = "", cex = 1.2, cex.lab = 1.3)
segments(x0 = df.sp$mean.x, x1 = df.sp$mean.x,
         y0 = df.sp$mean.y+df.sp$sd.y,
         y1 = df.sp$mean.y-df.sp$sd.y,
         lwd = 5*df.sp$sd.y/max(df.sp$sd.y),col =
bim.col[as.numeric(df.sp$TRP_TMP)])
legend("bottomright", c("Tropical","Temperate", "Others", "No
information"),
       pch = 20, title = "Origin",
       col = bim.col)
mtext("(b)",3,adj = 0, line = 0.5, cex = 2)


#### Correlation plot Niche length (Native vs Taiwan) ####
windows()
length.TW <- df.sp$sd.y*2
```

```
length.Nat <- df.sp$sd.x*2
plot(length.TW ~ length.Nat, pch = 20, col = "grey", las = 1,
     xlab = bquote("Niche length in native range ("~degree~"C)"),
     ylab = bquote("Niche length in Taiwan ( "~degree~"C)"),
     xlim = c(0,22), ylim = c(0,22))
cor.test(df.sp$sd.y, df.sp$sd.x) # not sig

#### 3-3-3 boxplot with climatic zone ####
names <- df.sp$TRP_TMP
value <- df.sp$dif
data <- data.frame(names,value)

# Basic boxplot
windows()
BP.trptmp <- boxplot(dif ~ TRP_TMP, data = df.sp, notch = T,
        las = 1, xlab = "Origin", ylab = bquote("Deviation ("~degree~"C)"),
        names = c("Tropical","Temperate", "Others", "No information"),
cex.lab = 1.5, col = bim.col)
mtext(paste0("(",BP.trptmp$n,")"), side = 1, at = 1:4, line = 2)
title(main = "(b)", font.main = 1, adj = 0, line = 0.5, cex.main = 2)
# Add data points
mylevels <- levels(data$names)
levelProportions <- summary(data$names)/nrow(data)
for(i in 1:length(mylevels)){

  thislevel <- mylevels[i]
  thisvalues <- data[data$names==thislevel, "value"]

  # take the x-axis indices and add a jitter, proportional to the N in each
level
  myjitter <- jitter(rep(i, length(thisvalues)),
amount=levelProportions[i]/2)
  points(myjitter, thisvalues, pch=20,cex = 0.7)

}
#### 4. linear regression (dif) ####
#### 4-1 Usage, n = 252 ####
```

```
windows(width = 14, pointsize = 20)
par(mfrow = c(1,3))
# PCA ordination diagram
biplot(PCA.usg, display = "species",
       xlab = "PC1 (47.7%)", ylab = "PC2 (29.6%)",
       main = "Usage", cex.lab = 1.2) # PC1: pretty vs useful # PC2:
Medicinal vs non-medicinal
# regression of deviations on usg 1st axis
title(main = "(a)", font.main = 1, adj = 0, line = 0.5, cex.main = 2)
lm.usg1 <- lm(dif ~ usgPC1, data = df.sp)
summary(lm.usg1) # Adjusted R-squared:  0.0207 # p-value < 0.05
plot(dif ~ usgPC1, data = df.sp, ylab = expression("Deviation
("~degree~"C)"),
     cex.lab = 1.2)
abline(lm.usg1, col = "red")
text(0,14,bquote(atop("Adj "~R^2~"="~0.021,"P < 0.05")),adj = 0, cex = 1.2)
title(main = "(b)", font.main = 1, adj = 0, line = 0.5, cex.main = 2)

# regression of deviations on usg 2nd axis
lm.usg2 <- lm(dif ~ usgPC2, data = df.sp)
summary(lm.usg2) # Adjusted R-squared: 0.0043 # p-value > 0.05
plot(dif ~ usgPC2, data = df.sp, ylab = expression("Deviation
("~degree~"C)"),
     cex.lab = 1.2)
title(main = "(c)", font.main = 1, adj = 0, line = 0.5, cex.main = 2)

#### 4-2 Residence time, n = 376 ####
lm.resid <- lm(dif ~ year, data = df.sp)
summary(lm.resid) # Adjusted R-squared:  -0.001815 # p-value > 0.05
windows()
plot(dif ~ year, data = df.sp, xlab = "Year", ylab = expression("Deviation
("~degree~"C)"),
     pch = 20, col = "grey", main = "Residence time", cex.lab = 1.2)

#### 4-3 Biome, n = 388 ####
# plot Tukey mean separation results
df.sp$MajorBiome <- as.factor(df.sp$MajorBiome)
aov.bim <- aov(dif ~ Abbreviation, data = df.sp)
```

```
summary(lm(dif ~ MajorBiome, data = df.sp)) # 0.623
Tukey <- TukeyHSD(aov(dif ~ Abbreviation, data = df.sp), order = T)
star.bim <- Tukey$Abbreviation[,4] %>% gtools::stars.pval()
windows()
par(mar = c(1, 6, 2, 2) + 0.1)
plot(Tukey, las = 1, cex.axis = 0.6)
text(x = rep(-10,length(star.bim)), y = length(star.bim):1 , labels =
star.bim, col = "red")
# box plot
windows()
BP <- boxplot(dif ~ BiomeID, data = df.sp, main = "Major native biome",
              col = bim.col[c(1,1,1,2,2,1,2,3,3,3,3,3)], ylim = c(-10,15),
              ylab = expression("Deviation ("~degree~"C)"), notch = T)
sample.size <- sapply(BP$n, function(x) paste0("(",x,")"))
mtext(text = sample.size, line = 2, side = 1, at = 1:12, cex = 0.8) #
number of species in this biome
legend("topright", col = c(2,4,8), legend = c("Tropical", "Temperate",
"Others"), pch = 15, bty = "n")
abline(h = 0, lty = 2, col = "grey")

summary(lm(dif ~ TRP_TMP, data = df.sp)) # Adjusted R-squared:  0.5687 # p-
value: < 2.2e-16
#### Optimum temperature range differ from bioclimatic origin ####
# in Native range
aov(sd.x ~ TRP_TMP, data = df.sp) %>% anova() # sig
aov(sd.x ~ TRP_TMP, data = df.sp) %>% TukeyHSD() # TMP-TRP not sig
t.test(df.sp$sd.x[df.sp$TRP_TMP == "TRP"],df.sp$sd.x[df.sp$TRP_TMP ==
"TMP"]) # sig P < 0.01


# in TW
t.test(df.sp$sd.y[df.sp$TRP_TMP == "TRP"],df.sp$sd.y[df.sp$TRP_TMP ==
"TMP"]) # sig p < 0.001


#### 5. alien species elevation range in TW ####
ele.range <-
read.csv("alien%20species%20elevation%20range%20in%20Taiwan.csv")
ele.range <- merge(ele.range, df.sp[,c("species","TRP_TMP")], all.x = T)
ele.range$TRP_TMP[is.na(ele.range$TRP_TMP)] <- "NA"
ele.range <- ele.range[order(ele.range$Ele_max, decreasing = T),]
```

```
# The elevation ranges and median elevation of occurrence
windows()
par(mfrow = c(1,2))
plot(0,4000, xlim = c(0,4000), ylim = c(0,nrow(ele.range)), type = "n",
     xlab = "Elevation (m a.s.l.)", ylab = "Species order")
title(main = "(a)", font.main = 1, adj = 0, line = 0.5)
for (i in 1:nrow(ele.range)) {
  segments(ele.range$Ele_min[i], i, ele.range$Ele_max[i], i)
}
for (i in 1:nrow(ele.range)) {
  points(ele.range$Ele_Med[i], col = "red", i, pch = 20)
}

# The relation between elevation range and maximum elevation
plot(Ele_length ~ Ele_max, data = ele.range, xlab = "Maximum elevation (m
a.s.l.)",
     ylab = "Elevation length (m a.s.l.)", pch = 20, col =
bim.col[as.numeric(ele.range$TRP_TMP)], cex = 0.8)
title(main = "(b)", font.main = 1, adj = 0, line = 0.5)
legend("topleft", c("Tropical","Temperate", "Others", "No information"),
       pch = 20, title = "Origin",
       col = bim.col)
t.test(ele.range$Ele_max[ele.range$TRP_TMP == "TRP"],
       ele.range$Ele_max[ele.range$TRP_TMP == "TMP"]) # max ele different #
P < 0.001

ele.range[ele.range$Ele_max>2000 & ele.range$Ele_length < 1000,]
#                species Ele_min Ele_max  Ele_Med Ele_length TRP_TMP
# 311      Poa trivialis    1997    2573 2187.000        576     TMP
# 49    Bellis perennis    2188    2515 2247.000        327     TMP
# 163 Eutrema japonicum    1395    2367 2051.667        972     TMP
# 365 Solanum tuberosum    1518    2152 1889.750        634     TRP
ele.range[ele.range$Ele_max>2500 & ele.range$Ele_length < 2000,]
```