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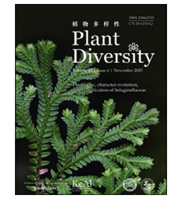

Research paper

Effects of land-use types and the exotic species, *Hypochaeris radicata*, on plant diversity in human-transformed landscapes of the biosphere reserve, Jeju Island, Korea

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A B S T R A C T

Land-use and plant invasion influence biodiversity. Understanding the effects of land-use types and invasive plants on the ecosystem is crucial for better management and the development of strategic plans for increasing biodiversity in Jeju Island, Korea, a designated Biosphere Reserve by the United Nations Education, Scientific, and Cultural Organization. The effect of the most dominant invasive exotic species, *Hypochaeris radicata*, on the four land-use types of Jeju Island was investigated. Plant composition, soil characteristics, and plant diversity among four land-use types (cropland, green space, neglected land, and residential) were compared. Among the land-use types, croplands had the most diverse plant composition and the highest richness in exotic and native plant species. Croplands, such as tangerine orchards, which are widely distributed throughout Jeju Island, showed the highest plant diversity because of medium intensity disturbance caused by weed removal. The relative cover of *H. radicata* did not differ between land-use types. However, *H. radicata* invasion was negatively related with plant species richness, making this invasive species a threat to the biodiversity of native herbs present in land-use areas. *H. radicata* adapts to areas with a broad range of soil properties and a variety of land-use types. Therefore, it is crucial to monitor land-use types and patterns of plant invasion to guide the implementation of consistent management and conservation strategies for maintaining ecosystem integrity of the transformed habitat in Jeju Island.

1. Introduction

The world's ecosystems changed more rapidly in the 20th century than at any other time in human history, causing species extinction to accelerate exponentially (Habibullah et al., 2022). Biodiversity loss is driven by overexploitation (Souza and Prevedello, 2020), biological invasion (Linders et al., 2019), anthropogenic pollution (Maiti and Chowdhury, 2013), land disturbance, and climate change (Visconti et al., 2016). Land use causes the fragmentation of natural or semi-natural habitats and is therefore considered to be the most significant anthropogenic threat to biodiversity (Dullinger et al., 2020; García-Vega and Newbold, 2020). This remains true even with increased interest in effects of climate change (Dullinger et al., 2020). The impacts of land-use type and land cover on vegetative composition and plant diversity remain largely unexplored (Aneva et al., 2020).

Land use patterns cam affect the frequency and impact of biological invasions (Vilà and Ibáñez, 2011). Land-use changes, such as transformation of natural ecosystems to agricultural systems, modify ecosystem functions, such as water demand, soil characteristics, and habitat quality, which in turn facilitate biological invasions (Gerlach, 2004; Manzoor et al., 2021). The impact of invasive species on native plant diversity is determined in part by the modification, degradation, and extent of habitat loss (Didham et al., 2007; González-Moreno et al., 2013). Habitat disturbances play fundamental roles in plant community structure. The success of invasive plants is strongly linked to such disturbances by

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historical and present patterns of land use and development (Pellegrini et al., 2021).

Understanding these relationships can inform conservation and management efforts (Bradley and Mustard, 2006; Meyfroidt et al., 2022). In developing conservation strategies for reserves, the detection and mitigation of effects of invasive species need to be addressed with high priority (Xu et al., 2017; Wang et al., 2022). Land use and plant invasion should be considered together to better understand plant biodiversity.

Invasive species attract worldwide attention because they cause major environmental damage, contribute to the loss of biodiversity (Kumar Rai and Singh, 2020), and have a detrimental impact on human activities and health (Mazza et al., 2014). Invasive exotic plants result in the loss of ecosystem function and the extinction of native species, which reduces native biodiversity and causes a corresponding decline in socioeconomic status (Samways et al., 1996; Marbuah et al., 2014). Invasive species replace or reduce population sizes of native species, which can result in localized biodiversity loss (Peh, 2010).

Hypochaeris radicata, commonly called flatweed, is an invasive plant which has colonized all continents (Ortiz et al., 2008). It represents the dominant invasive plant on Jeju Island, Republic of Korea (Ryu et al., 2017), where the climate allows it to overwinter in the form of an evergreen rosette (Park, 2022). Although Jeju Island is designated a Biosphere Reserve, its rapidly expanding human population and the island's attractiveness as a center of tourism have put its natural resources under severe pressure (Hong et al., 2021). In addition, climate change has had more adverse effects on Jeju Island than in mainland Korea (Lee et al., 2013).

Previous studies have reported the distribution of *H. radicata* on Jeju Island (Ryu et al., 2017; Lee et al., 2018; Kim et al., 2020a). Adhikari et al. (2019) predicted the potential impact of climate change on plant invasion in the Republic of Korea, including Jeju Island, and Hong et al. (2021) monitored loss of habitat quality on Jeju island. However, there has been no in-depth research focusing on the relationship between an invasive exotic species and human-transformed landscapes. Furthermore, previous studies did not consider the relationship between land-use types and plant biodiversity. Therefore, research on invasive exotic plants is essential for understanding the dynamics of ecological communities (Song et al., 2018b) and for predicting future invasion events, such as the dispersion of plant species from Jeju Island to the Korean mainland in the near future (Adhikari et al., 2019). In particular, research that monitors how habitat quality and land use affect plant biodiversity and exotic species invasion is required.

Here, we hypothesized that land-use types in the transformed ecosystem of Jeju Island influence plant composition, soil characteristics, and plant diversity. This hypothesis was addressed by examining differences in plant composition, plant diversity, and soil environmental factors among four land-use types. Also, we assessed the relationship between the relative cover of the invasive exotic species, *H. radicata*, and exotic and native plant species richness.

2. Material and methods

2.1. Study species

H. radicata L. is a global weed species native to Europe that has rapidly spread to the Americas (Luteyn et al., 1999), Asia (Ng and Driscoll, 2014), Australia (Pickering and Hill, 2007), New Zealand (Esler, 1988), and the Pacific Islands (Pickard, 1984). The species was accidently introduced into Jeju Island during the 1980s (Sun et al., 1992), where its detrimental effects, such as its invasion of native plant habitats and economic damage to farmland (Park, 2022), led to it being designated by the Korean Ministry of Environment as a harmful species in 2008 (Lee et al., 2011).

2.2. Study area

This study was conducted on Jeju Island (33°10′–33°34′ N, 126°10′–127° E) in the Republic of Korea, which is located in the southernmost part of the Korean peninsula. From 1991 to 2020, the average annual temperature and precipitation of Jeju Island was 16.2 °C and 1502.3 mm, respectively (Ryu et al., 2017; KMA, 2021). Jeju Island has the tallest mountain (Mt. Halla) in Republic of Korea (1950 m) and is a habitat for 3175 species, of which 51 are classified as endangered (Lee and Miller-Rushing, 2014). The biodiversity of Jeju Island is important because nature-based tourism, which is the island's main industry, depends on the island having rich species diversity and diverse ecosystems (Kim et al., 2020b). Jeju Island is the only site in the world to be designated as a Biosphere Reserve (2002), World Natural Heritage Site (2007), and Global Geopark (2010) (Kim et al., 2018b). Being a triple crown winner, Jeju Island is a popular destination for domestic and international tourists. In 2019, 15, 286, 136 tourists visited Jeju Island, representing a 6.8% increase on the previous year (Jeju Tourism Organization, 2020). The biodiversity of Jeju Island is threatened by exotic species invasion (Lee et al., 2018), and the island has suffered a 24.9% loss of natural habitat between 1989 and 2019. Habitat quality has decreased by 15.8% because of land development activities associated with increased tourism (Kim et al., 2018a; Hong et al., 2021).

2.3. Sampling design and analysis

Specific land-use types were determined by field investigations. Land use was classified into four types: i) cropland, ii) green space, iii) neglected land, and iv) residential. The main crops on Jeju Island are tangerine, bean, garlic, Alpine radish, and carrot (Jang et al., 2019). Tangerine orchards are most common, predominant in 10 among 13 sites (almost 77%) of the croplands we surveyed. As about 99% of farms in Jeju grow tangerines, this crop comprises more than 50% of the outdoor cultivated area excluding greenhouses (Kim and Ko, 2022). Cropland thus refers mainly to tangerine orchards. Neglected land refers to open, abandoned, or unused spaces between buildings or fields. Green space represents natural grassland or shrubland, which are unmanaged.

Vegetation composition was randomly surveyed in 13 croplands, 39 green spaces, 23 neglected lands, and 40 residentials for a total of 115 sites (Fig. 1). We tried to include all areas of Jeju municipality, which covers the northern half of Jeju Island (except for Mt. Halla, which is located in the middle of the island). Thirty to 40 sites of each land-use type were initially selected in January, 2016 for monitoring. However, mostly tangerine field data were available for assessing cropland species diversity as heavy herbicide use effectively reduced other sites to monocultures. Also many neglected lands were lost during the study because of rapid real-estate development during the sampling period (Chu, 2017). As price of houses increased rapidly in 2016, many small apartment buildings were built on previously neglected land. Representative pictures of land use types are presented in Supplemental File S1 in Appendix A. All herbs (excluding shrubs and trees) were identified to the species level during the 2016 and 2017 *H. radicata* blooming season (May to July) using ten quadrats (1 m^2; 5 m apart) for each of the 115 sites, which were selected randomly. The species richness of vegetation was defined as the number of plant species recorded in each quadrat (1 × 1 m) (Han et al., 2021). The percentage of cover of all the species in each quadrat was visually estimated following the methods of Son et al. (2020) and evenness (Hill's Index) was calculated (Hill, 1973).

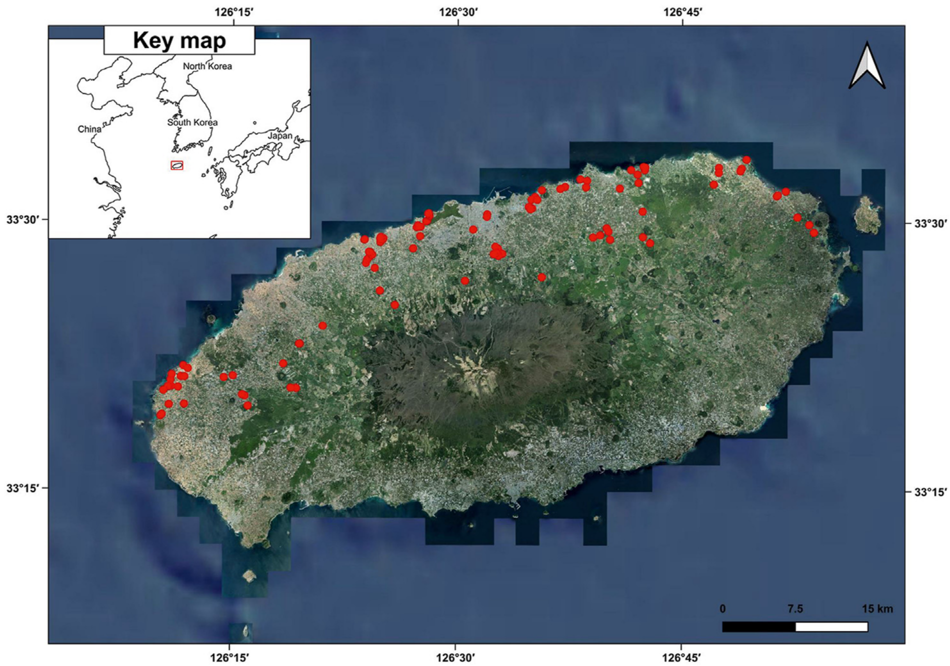

Fig. 1. Satellite image of Jeju Island. Red dots mark the locations of the 115 surveyed sites. The satellite image was acquired from the Spatial Information Open Platform, Vworld (https://map.vworld.kr/map/ws3dmap.do).

Simultaneous with vegetation surveys, soil samples were collected from each of the 115 sites to quantify soil characteristics. Soil was taken from three locations (upper left, middle, lower right) per sampling site using a soil auger (corer dimensions: 5 cm diameter and 5 cm depth). The collected soil from the three locations within each sampling site was mixed thoroughly to produce a composite sample. Soils were evaluated by quantifying total carbon (C) and nitrogen (N) using an element analyzer (EA1110; CE Instruments, UK). Cations of the soil (calcium, potassium, sodium; phosphorous and zinc) were determined using an inductively coupled plasma (ICP) atomic emission spectrometer (ICP-730ES) at the National Center for Inter-University Research Facilities, Seoul National University.

2.4. Data analysis

Statistical analyses were performed in the R software environment (R Core Team, 2019) using the "vegan" package for multivariate and diversity analyses (Oksanen et al., 2019). The generalized linear models (GLM) function was used for comparison of plant species richness, exotic and native species richness, species evenness, and soil characteristics among land-use types. Also, GLM was fitted to verify the effect of *H. radicata* on plant diversity.

Vegetation community data were analyzed using both multivariate and univariate methods. To describe the differences in plant species composition among the four land-use types, permutational multivariate analysis of variance was performed with the function "Adonis" (Oksanen et al., 2019). Species with relative cover under 30% were excluded from the analysis. The cover values of 65 species were subjected to double square root transformation ($\sqrt{(\sqrt{\text{cover}+1})}$) to reduce the influence of dominant and rare species (Pajunen et al., 2012). Detrended correspondence analysis (DCA) using Bray–Curtis dissimilarities was performed, and the deviational ellipses of land-use ('ordiellipse' function) were plotted in the ordination space to describe species compositional differences.

To present the soil characteristics related to vegetation and land-use types, certain variables (i.e., Mg and N) that were highly correlated with other factors (i.e., Na and C) ($r > 0.75$) were removed using Pearson's Correlation. This resulted in the reduction of the number of predictive variables according to variance size (Dormann et al., 2013; Son et al., 2017). Principal component analysis (PCA) was performed, and the significant ($p < 0.05$) variables were plotted. GLM was used to verify differences in soil characteristics and plant diversity among land-use types. Tukey's honestly significant difference (HSD) multiple comparison test was used to determine statistically significant differences among land-use types.

Finally, the effect of *H. radicata* on plant species richness, and exotic and native plant species richness, was tested using GLM with Poisson error distribution (Gea-Izquierdo et al., 2007; Muthukrishnan et al., 2018), and the data were fitted with a trend line.

3. Results

The survey of vegetation in the four land-use types found 219 plant species from 54 families distributed as follows: 122 plant species in croplands, 130 in green spaces, 82 in neglected lands, and 99 in residential areas. There were 143 (65.3%) native, 62 (28.3%) exotic, and 14 (6.4%) cultivated plants. The most abundant species were *H. radicata* (also known as flatweed), *Artemisia dubia* (mugwort), *Erigeron annuus* (daisy fleabane), *Trifolium repens* (white clover), *Poa sphondylodes*, *Oxalis corniculata* (creeping woodsorrel), *Artemisia princeps* (Korean wormwood), and *Cerastium glomeratum* (sticky mouse-ear chickweed). Among the eight most abundant species, four, namely, *H. radicata*, *E. annuus*, *T. repens*, and *C. glomeratum*, were exotic.

3.1. Plant compositional differences by land-use type

DCA of all land-use types represented a distinct separation of the cropland type ($r^2 = 0.1296$, $p < 0.001$) (Fig. 2). This analysis revealed that species composition in croplands differed from that of the other three land-use types. Cropland sites fell primarily along

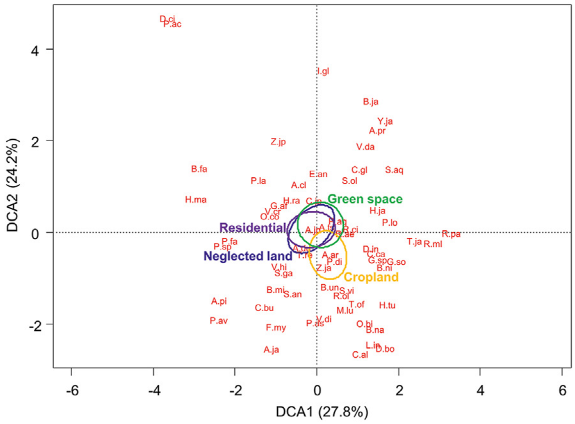

Fig. 2. Detrended correspondence analysis (DCA) ordination diagram for the first two axes showing plant species compositional differences among the four land-use types of Jeju Island. Only species having a sum of cover of more than 30% are shown. Species are abbreviated using the first letter of the generic name and the first two letters of the species names. For example, the full scientific name of A. pr in the green space quadrant is *Artemisia princeps*, while H. ra refers to *Hypochaeris radicata*. Full scientific names of the species are listed in Supplemental File S2 in appendix A.

the lower central part of the second DCA axis. The first two axes accounted for 27.8% and 24.2% of variation in plant data.

3.2. Differences in soil characteristics by land-use type

Principal component axis-1 (PC1) and axis-2 (PC2) accounted for 87.7% and 8.2% of the total variance in the dataset for soil characteristics, respectively (Fig. 3). Croplands were well discriminated by PC1 from other land-use types. All soil environmental factors correlated ($p < 0.05$) with either PC1 or PC2. Soil characteristics, such as Ca, K, Na, and Zn content, had positive relationships to croplands. The concentrations of Ca (17,065 ± 3605 mg kg^{-1}, mean ± S.E), Na (833 ± 159 mg kg^{-1}, mean ± S.E), and Zn (58 ± 8 mg kg^{-1}, mean ± S.E) in the croplands were significantly higher than those of other land-use types ($p < 0.05$) (Table 1).

3.3. Diversity and exotic species presence among land-use types

Croplands showed a significantly higher species richness value (24.3 ± 3.4, mean ± S.E) than those of other land-use types (Fig. 4a). Differences in species richness among green space (10.7 ± 0.7), neglected land (10.6 ± 0.9), and residential (9.2 ± 0.7) were not statistically significant (Fig. 4a). Furthermore, there were no statistical differences in species evenness among land-use types. Croplands, neglected lands, residentials, and green space had species evenness values of 0.90 ± 0.01, 0.83 ± 0.02, 0.83 ± 0.01, and 0.82 ± 0.02, respectively (Fig. 4b). Exotic (8.9 ± 1.4) and native (14.5 ± 2.0) species richness of croplands were significantly greater than those of other land-use types (Fig. 5).

3.4. Effect of H. radicata on diversity and exotic species

The relative cover of *H. radicata* was not significantly different among land-use types ($p > 0.05$; Fig. 6). In addition, soil characteristics (i.e., C, Ca, K, N, Na, Total phosphorus, and Zn content) and land-use types did not affect the relative cover of *H. radicata* based on GLM ($p > 0.05$). Although the median of *H. radicata* was lowest in croplands, there were no differences in the mean relative cover of *H. radicata* among the four land-use types. The relative cover of *H. radicata* affected total plant species richness, and exotic and native plant species richness negatively. Richness values decreased as the relative cover of *H. radicata* increased ($p < 0.001$; Fig. 7).

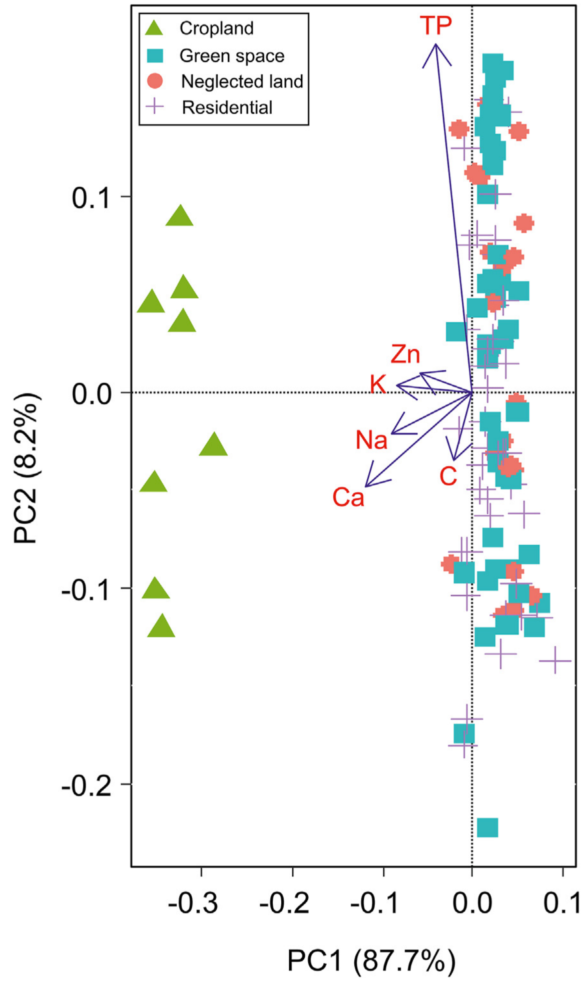

Fig. 3. Principal component analysis (PCA) ordination diagram showing the distribution of soil carbon and selected elements in different land-use types. C, carbon; Ca, calcium; K, potassium; Na, sodium; TP, total phosphorous; Zn, zinc.

4. Discussion

4.1. General flora and vegetation

H. radicata is managed because it is designated as a harmful species by the Ministry of Environment, Korea (Hwang et al., 2019). However, *H. radicata* is found only in the southern part of the Korean Peninsula and Jeju Island, and the active invasion area is limited at present to Jeju Island. Because the dominance and invasiveness of this species in Jeju Island is overwhelming (Park, 2022), it was designated as a harmful species based only on its occurrence and effects on Jeju Island. In this study, we found that *H. radicata* showed the highest vegetation coverage across all land types. *H. radicata* has become the most common plant throughout Jeju Island (Ryu et al., 2017). Possibly its competitive dominance results from its blooming in May and June, earlier than most native plant species, so it takes a foothold on the island, displacing other species. The study of *H. radicata* in Jeju Island thus more generally provides insight into the means b which invasive alien plants spread and displace native species.

We identified 219 plant species from 54 families. Croplands, green spaces, neglected lands, and residential areas had 122, 130, 82, and 99 plant species, respectively. Vascular plants in the Republic of Korea and Jeju Island belong to 4596 and 1990 taxa, respectively (Kim, 2009a; NIBR, 2022), confirming the rich plant

Table 1
Soil characteristics of four land-use types.

	Cropland	Green space	Neglected land	Residential
Number of sites	13	39	23	40
C (%)	4.6 (±0.7)	4.0 (±0.6)	3.1 (±0.5)	2.7 (±0.3)
N (%)	0.40 (±0.11)	0.30 (±0.05)	0.25 (±0.05)	0.21 (±0.03)
Ca ($mg \cdot kg^{-1}$)	17,065 (±3605)[b]	10,291 (±1391)[a]	9292 (±1479)[a]	11,624 (±1216)[a]
K ($mg \cdot kg^{-1}$)	1227 (±167)	1257 (±95)	1444 (±184)	1325 (±122)
Na ($mg \cdot kg^{-1}$)	833 (±159)[b]	440 (±63)[a]	322 (±47)[a]	500 (±57)[a]
TP ($mg \cdot kg^{-1}$)	98 (±19)	145 (±33)	255 (±70)	149 (±30)
Zn ($mg \cdot kg^{-1}$)	58 (±8)[b]	30 (±2)[a]	31 (±4)[a]	34 (±4)[a]

Values represent mean ± standard error. Different letters mean significant differences according to Tukey's HSD multiple comparison test ($p < 0.05$). C, carbon; Ca, calcium; K, potassium; Na, sodium; TP, total phosphorous; Zn, zinc.

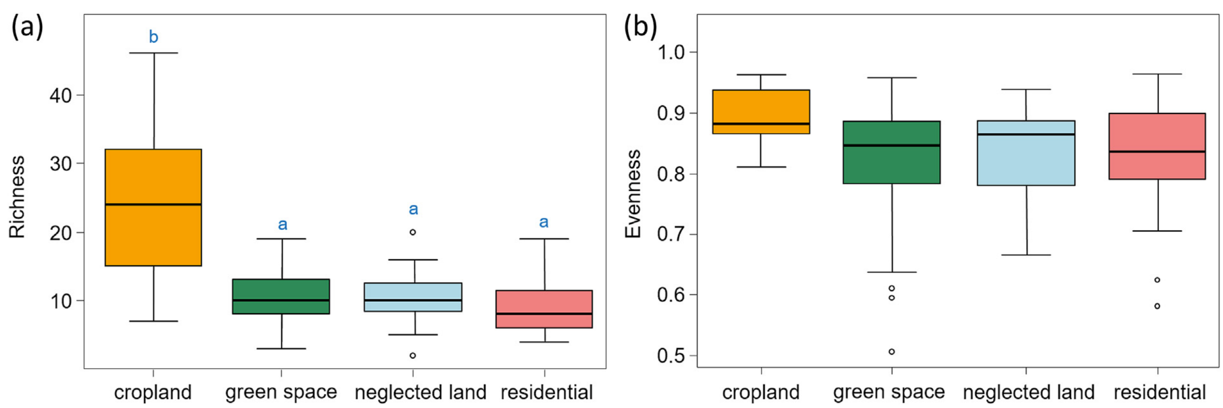

Fig. 4. Boxplots for (a) species richness and (b) species evenness among land-use types. Each boxplot represents results for croplands (n = 13), green space (n = 39), neglected land (n = 23), and residential (n = 40). Black lines within the boxes indicate the median. Box boundaries correspond to the 25th and 75th quartiles, and whiskers refer to the 10th and 90th percentiles. Open circles are outliers. Different letters mark significant post-hoc differences among land-use types (Tukey test, $p < 0.05$).

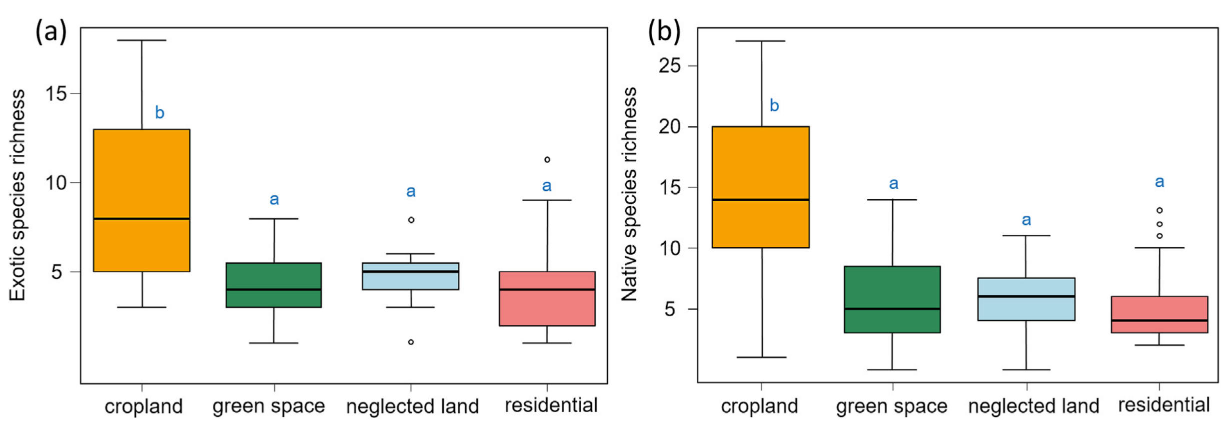

Fig. 5. Boxplots for (a) exotic species richness and (b) native species richness among land-use types. Each boxplot represents results for croplands (n = 13), green space (n = 39), neglected land (n = 23), and residential (n = 40). Black lines within the boxes indicate the median, box boundaries refer to the 25th and 75th quartiles, and whiskers indicate the 10th and 90th percentiles. Open circles are outliers. Different small letters mark significant post-hoc differences among land-use types (Tukey test, $p < 0.05$).

diversity and habitat quality of these regions (ME, 2012; Hong et al., 2021). Jeju Island also has a diverse community consisting of grasslands, temperate and subtropical forests, and marine areas (Lee and Miller-Rushing, 2014). Its unique plant community system arose independently of that of mainland Korea. The composition of its vegetation is shaped by the distinct environments of this volcanic island and its oceanic climates (Kim et al., 2020a).

The vegetation of the 115 sites studied consisted of a high number of exotic species (62 taxa, 28.3%), of which *H. radicata* was predominant. Among the eight most abundant plant species, four were exotic plants. Jeju Island's mild climate throughout the year, its intensive land development, foreign trade, and tourism (Ryu et al., 2017; Adhikari et al., 2019) all likely contribute to the richness of invasive exotic plants. Also, Jeju Island is a prime naturalization center for imported exotic plant species, which account for about 76% of the 334 domestically introduced species (NIE, 2017; Ryu et al., 2017). Moreover, 90 taxa of the 134 Korean endemic plants that are endangered inhabit Jeju Island (UNESCO, 2018). Since its designation as a Biosphere Reserve by UNESCO (United Nations Educational, Scientific and Cultural Organization), the introduction of invasive exotic species and frequent land development devastated the island's original plant ecosystem (Lee et al., 2018).

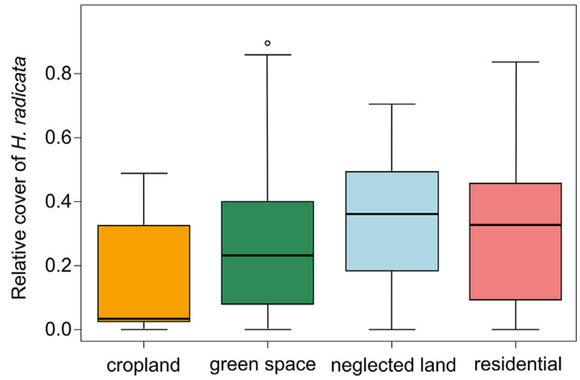

Fig. 6. Boxplots for relative cover of *Hypochaeris radicata* among land-use types. Black lines within the boxes indicate the median, box boundaries refer to the 25th and 75th quartiles, and whiskers indicate the 10th and 90th percentiles. Common small letters indicate no statistical differences among land-use types (Tukey test, $p < 0.05$).

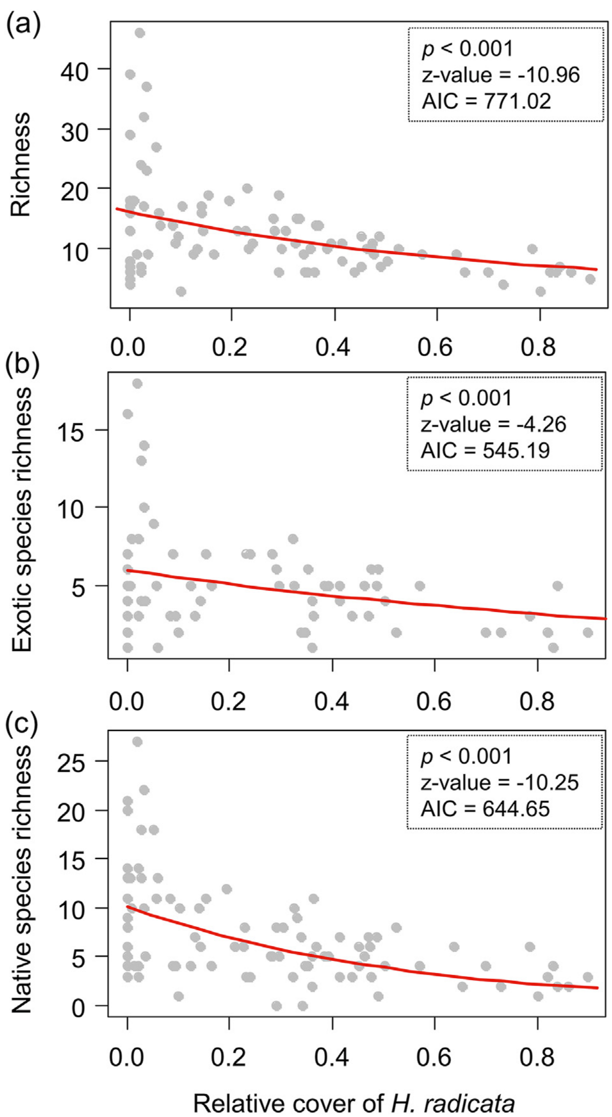

Fig. 7. The relationship between the relative cover of *Hypochaeris radicata* and (a) species richness, (b) exotic species richness, and (c) native species richness. Trend lines are shown for significant relationships ($p < 0.001$).

Jeju Island has the highest number of exotic plants in the Republic of Korea (NIE, 2017; Adhikari et al., 2021). Many of these invasive exotic plant species are native to tropical countries and thus have a high critical thermal maxima. As such, they should thrive in higher temperatures brought about by climate change (Adhikari et al., 2019; Sintayehu et al., 2020). Based on these results, the biodiversity of Jeju Island is threatened by exotic tropical and subtropical plant propagules introduced by tourism, transportation, and international trade (Paiaro et al., 2011). If left unattended, Jeju Island's plant dieristy will likely decline even further.

4.2. Plant composition, plant diversity, and soil characteristics in different land-use types

Croplands had higher plant species richness, both of exotic and native species, than those of green spaces, neglected areas, and residentials, even with the smallest number of sampling sites. Therefore, croplands may be the best indicators of plant diversity and plant community composition. This is in contrast to the results of Aneva et al. (2020) who showed that the lowest plant diversity occurs in land-use types representing annual cropland, such as corn and sunflower, or in fallow land. Also, agricultural activity is considered one of the main factors causing loss of biodiversity globally (Kleijn et al., 2009).

Our results demonstrate the unique characteristics of agricultural activities on Jeju Island. Lands where crops are managed by farming operations including weed removal during the growing season suffer from soil disturbance. Weed management, which involves removal, mowing, herbicide application, and burning, can have positive, neutral, and negative effects on plant diversity (Martín-Forés et al., 2017; Connolly et al., 2018; Song et al., 2018b). The impact of weeding on plant diversity depends on the weed species, biodiversity variables, and method of weed removal (Wotton and McAlpine, 2012). Weed control usually encourages settlement by the same or other species because of trampling, soil disturbance, fertilizer addition, and increased light availability (Pavlovic et al., 2009; Wotton and McAlpine, 2012; Song et al., 2018b). Kershaw and Mallik (2013) found that the Intermediate Disturbance Hypothesis predicts how disturbance predicts species diversity in upland sites with medium to high productivity. One particular example is tangerine orchards (croplands), which occupy a large part of the area (~209 km^2) devoted to crops (Jung and Kawamura, 2011; Song et al., 2013). Depending on the weed species and density, both the Weed Control Program and the Weed Management Program recommend to use 3 to 5 herbicide application per year in citrus orchards (Buker, 2005). Because tangerine orchards require medium intensity management, croplands have higher plant diversity than those of other land-use types.

While urban land and cropland increased by 0.6- and 1.7-fold, respectively, natural habitats decreased by 24.9% from 1989 to 2019 in Jeju Island (Hong et al., 2021). The increase in croplands with high plant diversity is not linked to an increase in biodiversity in Jeju Island, since higher plant richness in croplands is associated with higher exotic species richness. The expansion of *H. radicata* can be accelerated by deforestation and sporadic mowing because its growth is favored in sun-exposed areas (Park, 2022). To conserve and improve plant biodiversity in Jeju Island, preserving high plant diversity in natural ecosystems, such as green spaces, is vital. Monitoring of land-use changes and invasive exotic plants should be performed on a continuous basis.

In neglected lands where regular management is not implemented, it is likely that some species dominate, resulting in low species diversity. This finding is consistent with the results of

Uematsu et al. (2010), which show that plant diversity decreases with a low level of disturbance. Neglected lands are usually private and consist of fallow ground with low levels of management and weed removal. As such, these lands are rarely disturbed, which can lead to low plant diversity. Conversely, in residential lands, intense management, such as mowing and pruning, contributes to low biodiversity caused by habitat loss and changes in habitat quality (Uchida and Ushimaru, 2014; Norton et al., 2016). Some shrubs and trees (e.g., *Actinodaphne lancifolia*, *Pinus thunbergii*, *Sasa quelpaertensis*) are abundant in green spaces (Kim, 2009b; Park et al., 2018; Hong et al., 2019). However, this study only considered vascular herbs, which had lower diversity in green spaces than croplands.

We found that the soil characteristics of each land-use type statistically differed with respect to Na, Ca, and Zn contents. Similar to the results of this study, Kuhman et al. (2011) show that soil cation concentration (i.e., K, Ca, Mg) correlates with the presence and abundance of invasive plants in historic agricultural sites. Croplands, which have high total plant species richness, and exotic and native plant species richness, are likely managed with chemical fertilizers even though total phosphorus concentration does not differ among land-use types. Jeju Island was formed by cumulative and sequential volcanic eruptions (Song et al., 2018a). Therefore, soil nutrients on the island are easily leached by run-off, leading to low soil fertility (Harcombe, 1980). Groundwater in Jeju Island is the sole source of fresh water because of the absence of perennial streams and is used extensively for cropland irrigation (Choi and Lee, 2012). Increased irrigation results in higher soil salinity of croplands than other land-use types because increases in irrigation inevitably lead to increases in soil salinity (Oosterbaan, 1997).

In addition to soil characteristics, establishment and distribution of exotic and native plants are determined by factors such as temperature (Gantchoff et al., 2018), elevation (Fontana et al., 2020), net primary productivity (Seabloom et al., 2006), population, and economic activities (e.g., real estate gross state product) (Taylor and Irwin, 2004). Future studies should take into consideration other soil characteristics, as mentioned above.

4.3. Relationships between H. radicata and plant diversity

H. radicata is the most dominant invasive plant on Jeju Island. The relative cover of this exotic plant species did not differ among land-use types. The uniform distribution of *H. radicata* on the island (Ryu et al., 2017) suggests that the relative cover of *H. radicata* is not influenced by soil characteristics nor land-use types. On Jeju Island, *H. radicata* is most prevalent in areas with frequent sporadic physical disturbance, such as roadsides and grasslands (Ryu et al., 2017). Turkington and Aarssen (1983) found that this species is tolerant to nutrient-deficient soils, particularly those that are deficient in phosphate. In addition, this species is frequently found in several habitats, such as cultivated fields, roadsides, sand dunes, abandoned areas, pastures, and lawns (Park, 2022), which is attributable to the eco-physiological characteristics of species with high tolerance to environmental conditions and competitiveness with other species (Mitchell and Bakker, 2014).

H. radicata develops stiff and wiry stems, prostrate rosettes, and buds that are close to the ground. These features shield the plant from mowing and grazing (Turkington and Aarssen, 1983). Also, *H. radicata* is drought resistant and has a deep tap root (Aarssen, 1981), which facilitates the rapid uptake and utilization of nitrogen (Schoenfelder et al., 2010). Therefore, *H. radicata* can dominate areas where environmental conditions are poor and diversity is low. However, it is possible that the relationship between poor environmental conditions and *H. radicata* abundance is causal. Gill et al. (2006) proposed that *H. radicata* takes up and coverts nitrogen more quickly than other plant species; however, it does not convert the nitrogen more efficiently into plant biomass and reproductive structures. Kim et al. (2005) showed that *H. radicata* has an allelopathy effect on crop plants such as Italian ryegrass and purple alfalfa. However, our study does not allow us to conclude which of the two hypothesis is correct, because we sampled only one year.

H. radicata is a wind-dispersed perennial weed (Ng and Driscoll, 2014). Plumed seeds of *H. radicata* have maximum dispersal distances that range from 2300 to 3900 m (Soons et al., 2004). As such, *H. radicata* is a pioneer species in highly disturbed habitats and can successfully colonize new land areas as an aggressive weed (Ortiz et al., 2008). The highly invasive nature of *H. radicata* threatens the ecosystem integrity of Jeju Island (Adhikari et al., 2019).

Although there were no significant differences in the relative cover of *H. radicata* among land-use types, species richness, exotic species richness, and native species richness decreased as the relative cover of *H. radicata* increased. Exotic species and native species richness were negatively related to the relative cover of *H. radicata*. Similar to our results, *H. radicata* was reported to have not only a wide horizontal and vertical growth range, but also to have a negative influence on local transformed ecosystems (Ryu et al., 2017; Hwang et al., 2019). To date, there is no effective way to control the dispersal of *H. radicata* (Hwang et al., 2019). Even the Mt. Halla National Reserve, which has an elevation of 1950 m and encompasses a subalpine region, is at risk of biodiversity loss caused by the spread of *H. radicata* (Ryu et al., 2017). Adhikari et al. (2019) also estimated the habitat expansion of this invasive plant species in highly elevated areas of Mt. Halla National Reserve. Furthermore, the discovery of *H. radicata* in Chungcheong and Jeolla shows that dispersal and settlement of this invasive plant species have already occurred in inland Korea (Hyun et al., 2018), which could be accelerated by global climate change. Park (2022) also reported that the expansion of *H. radicata* was significantly influenced by development projects, such as the construction of residential areas and transportation systems.

Although we studied one invasive alien species, we also considered land-use types in areas where this species is not dominant. Our results thus shed light on invasion–diversity relations for all areas. Furthermore, our results reveal the effects that a major invasive alien species, such as that *H. radicata*, can have on Jeju Island and presumably other localities with similar habitats. Climate change and increased disturbance are likely to accelerate the spread of this invasive species. Management responses should be based on studies of specific invasion mechanisms employed by each invasive species. We have illustrated this by our study of one invasive alien species. As knowledge accumulates from studies such as ours, more ecologically appropriate predictions and responses will be possible.

5. Conclusions

The biodiversity of Jeju Island, a UNESCO-designated Biosphere Reserve, is threatened by the increased introduction of exotic tropical and subtropical plant propagules by tourism, transportation, and international trade. Among land-use types, croplands, such as tangerine orchards, had the most diverse plant composition and the highest richness of exotic and native plant species because of medium intensity disturbance due to weed removal. The relative cover of *H. radicata* did not differ among land-use types. However, *H. radicata* invasion negatively affected plant species richness, making this invasive species a threat to the biodiversity of native herbs present in land-use areas. *H. radicata* adapts to areas having a broad range of soil properties and a variety of land-use types. Our data show that the highly invasive nature of *H. radicata* threatens the ecosystem integrity of Jeju Island.

Therefore, monitoring of land-use types and patterns of plant invasion provides the underpinning needed to develop and implement consistent management and conservation strategies for the maintenance of ecosystem integrity. While applicable to disturbed habitat on Jeju Island, these conclusions equally apply to other areas where *H. radicata* invasion is ongoing.

Author contributions

U.S. conceived the idea, collected the data, and revised the draft; B. S wrote and revised the manuscript. D.J.S. analyzed the data and wrote the manuscript.

Data statement

All the data sets and R codes are available from the corresponding author.

Declaration of competing interest

All the authors declare that they have no competing interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pld.2023.01.002.

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