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Major environmental factors and traits of invasive alien plants determine their spatial distribution: a case study in Korea

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Abstract

Background: As trade increases, the influx of various alien species and their spread to new regions are prevalent, making them a general problem globally. Anthropogenic activities and climate change have led to alien species becoming distributed beyond their native range. As a result, alien species can be easily found anywhere, with the density of individuals varying across locations. The prevalent distribution of alien species adversely affects invaded ecosystems; thus, strategic management plans must be established to control them effectively. To this end, this study evaluated hotspots and cold-spots in the degree of distribution of invasive alien plant species, and major environmental factors related to hot spots were identified. We analyzed 10,287 distribution points of 126 species of alien plant species collected through a national survey of alien species using the hierarchical model of species communities (HMSC) framework.

Results: The explanatory and fourfold cross-validation predictive power of the model were 0.91 and 0.75 as area under the curve (AUC) values, respectively. Hotspots of invasive plants were found in the Seoul metropolitan area, Daegu metropolitan city, Chungcheongbuk-do Province, southwest shore, and Jeju Island. Hotspots were generally found where the highest maximum summer temperature, winter precipitation, and road density were observed. In contrast, seasonality in temperature, annual temperature range, precipitation during summer, and distance to rivers and the sea were negatively correlated to hotspots. The model showed that functional traits accounted for 55% of the variance explained by environmental factors. Species with a higher specific leaf area were found where temperature seasonality was low. Taller species were associated with a larger annual temperature range. Heavier seed mass was associated with a maximum summer temperature > 29 °C.

Conclusions: This study showed that hotspots contained 2.1 times more alien plants on average than cold-spots. Hotspots of invasive plants tended to appear under less stressful climate conditions, such as low fluctuations in temperature and precipitation. In addition, disturbance by anthropogenic factors and water flow positively affected hotspots. These results were consistent with previous reports on the ruderal and competitive strategies of invasive plants, not the stress-tolerant strategy. Our results supported that the functional traits of alien plants are closely related to the ecological strategies of plants by shaping the response of species to various environmental filters. Therefore, to control alien plants effectively, the occurrence of disturbed sites where alien plants can grow in large quantities should be minimized, and the waterfront of rivers must be managed.

Keywords: Invasive alien plants, Functional traits, Habitat suitability, Hot spot, Species distribution model

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Background

As the economic costs of controlling and managing biological invasions have become increasingly severe in recent decades (Diagne et al. 2021), the governments of many countries have requested more efficient and practical management plans for invasive species. Thus, the demand has increased for systematic analyses of the nationwide distribution of alien plant species. Annually collected data from nationwide surveys on invasive species in South Korea provide an excellent opportunity to address these demands.

The distribution of invasive species is typically modeled using single species distribution models; however, this approach is not as suitable for analyzing community data containing multiple invasive species. Joint species distribution models provides a great opportunity to analyze such community data (Warton et al. 2015; Abrego et al. 2017) and can be used to determine hotspot and cold-spot areal distributions of invasive alien plants. Through identifying the hotspots of invasive alien plants, risk maps for more efficient management can be constructed. Local hotspot clusters may be associated with certain combinations of relevant abiotic factors, such as climate variables, topographic factors, and anthropogenic factors. The identification of these relationships could strengthen our understanding on how alien species invade new environments.

A key component of invasion science is understanding how the functional traits of invasive species respond to environmental filters or disturbances (Moullot et al. 2013; Cadotte et al. 2015; Pearson et al. 2018). When evaluating community datasets, species traits could be used as essential predictors to provide insights on why certain taxa are more abundant than others in the same environment. Therefore, including the interaction between the environment and traits could improve the power of the joint species distribution model.

Here, we aimed to analyze the nationwide distribution of invasive alien plants (IAPs) systematically to identify hotspots of occurrence and the environmental factors associated with these sites. We included the functional traits of the evaluated species to determine how these traits affect their responses to the environment. We used a spatial joint species distribution model with climatic variables, topographic variables, and disturbance-related variables, as well as functional traits and phylogenetic relatedness among species as predictors.

Materials and methods

Survey

The nationwide survey for the alien plant species was conducted by the National Institute of Ecology, South Korea, from 2015 to 2019. During this period, 20 scientists conducted convenient sampling in most provinces

(165 districts). At all survey points, the scientists set up temporary plots of variable sizes. In each plot, all alien plants were recorded. The scientists conducted a pilot survey on Jeju Island in 2015 and divided the mainland of Korea into three regions, surveying one region per year.

A total of 10,287 sampling points were obtained after cleaning the data. To analyze environmental factors, we collected 19 bioclimatic variables at a resolution of 30 arcs/second from WorldClim version 2 (Fick and Hijmans 2017) and ASTER GDEM version 3 at a resolution of 1 arc/second (NASA/METI/AIST/Japan Spacesystems and U.S./Japan ASTER Science Team 2019). We also recorded distance to rivers, distance to the sea, and road density within a 1-km circle of each plot. All environmental variables were resampled to a resolution of $10 \times 10 \text{ km}^2$.

All sample points were aggregated to a $10 \times 10 \text{ km}^2$ grid by pooling the recorded species to remove duplicates within a pixel of an environmental variable. The coordinates of the aggregated sampling points were recorded at the centroid of the original sampling points. The values of environmental variables were extracted by the aggregated sample points. Multicollinearity was removed by a stepwise procedure using the threshold of $\text{VIF} \leq 5$ in R package version 1.1.18 (Naimi et al. 2014). The selected variables were isothermality (bio 03), temperature seasonality (bio 04), maximum temperature of warmest month (bio 05), precipitation of driest month (bio 14), precipitation of warmest quarter (bio 18), distance to river, distance to sea, and road density. We only evaluated species that occurred at a frequency of more than 1% to remove rare species.

Functional traits

According to the Leaf-Height-Seed model proposed by Westoby (1998), functional traits related to leaf characteristics, plant height, and seed characteristics are essential factors for defining plant ecology strategy schemes. These traits are related to the efficiency of resource capture and utilization or competitive ability in various habitats (Diaz et al. 2016). We selected specific leaf area (SLA), leaf dry matter content (LDMC), plant height, and seed dry mass. These characteristics were relatively easy and largely obtainable from the functional trait database. Although morpho-anatomical (soft) traits, such as the variables we used, have lower predictive power than physiological (hard) traits, they can be used in combination to explain species responses along environmental gradients (Belluau and Shipley 2018).

We downloaded data on seed dry mass, SLA, and LDMC traits from the TRY database (Kattge et al. 2020). To summarize trait values among multiple measurements from multiple references, we first averaged trait

values per reference and species and calculated the median value per species. We inserted missing values using the median values of a species congeners to reduce data bias, where possible. Finally, 126 species were retained after listwise deletion for missing trait values.

Statistical modeling

We adopted the hierarchical model of species communities (HMSC) framework as a spatial joint species distribution model to explain which environmental factors are related to the occurrence of IAPs and their joint species richness (Fig. 1) (Ovaskainen et al. 2017; Tikhonov et al. 2020). We included the functional traits per species to analyze the contribution of functional traits to the level of species responses to environmental factors. Focal IAPs were phylogenetically related to each other; therefore, we incorporated phylogenies into the model to account for the non-independence of traits among taxa. A phylogenetic tree was constructed using the V.Phylo-Maker R package version 0.1.0, in which a mega-tree of 74,533 vascular plant species was provided (Jin and Qian 2019). The data were too spatially extensive to compute Bayesian JSDM; therefore, we used nearest neighbor Gaussian process (NNGP) approaches in the latent factor structure of HMSC (Tikhonov et al. 2019).

The HMSC framework used the following matrices to model the spatial context: spatial coordinates of the sampling unit, species occurrence at each sampling unit, environmental variables at each sampling unit, phylogenetic covariance matrix of focal species, and trait values of each species.

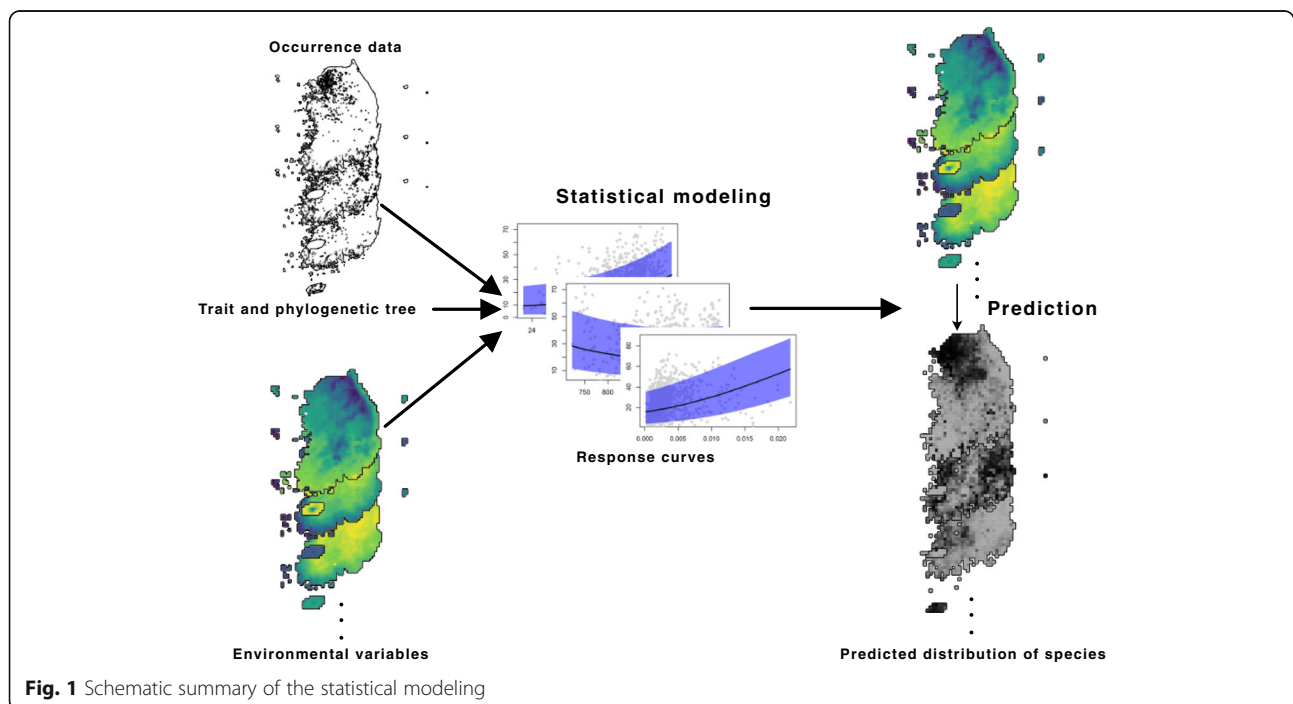
The sum of the predicted probability of all species represents the predicted species richness. For spatial cluster analysis, local Moran's I of predicted species richness was calculated for each pixel using queen contiguity-based weights (Anselin 1995) using the *spdep* R package version 1.1.5 (Bivand and Wong 2018). All analyses were performed in R 4.0.2 (R Core Team 2020).

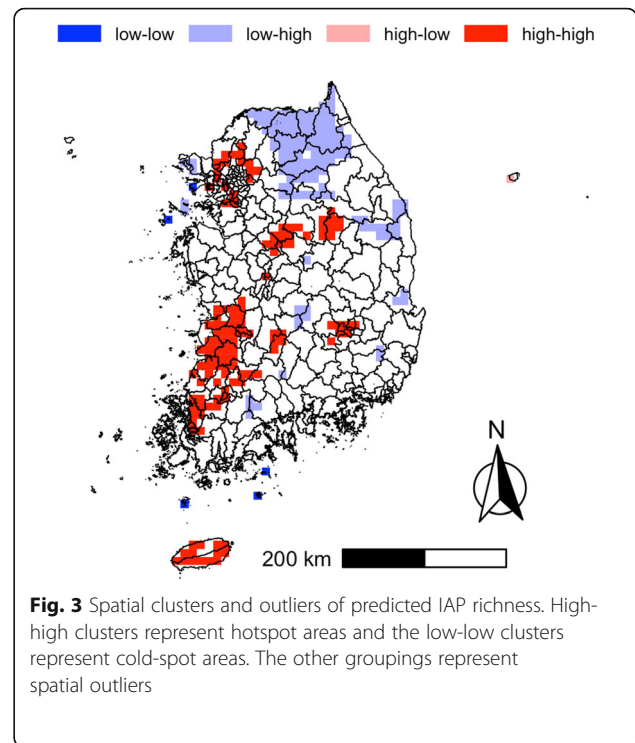
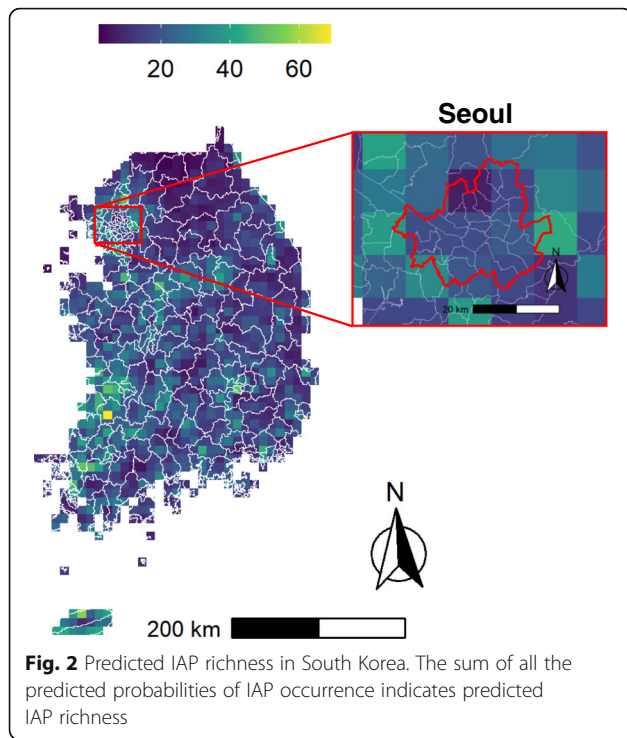
Results

The explanatory power of the model was evaluated using the AUC and Tjur's R-squared (Tjur 2009). The AUC was evaluated for each species (Table S1), and the average AUC was 0.910 ± 0.058 (mean \pm SD). Tjur's R squared was 0.27 ± 0.16 (mean \pm SD). The predictive power of the model was calculated by fourfold cross-validation, and the average AUC was 0.753 ± 0.101 (mean \pm SD). Tjur's R-squared was 0.12 ± 0.11 .

The richness of IAPs was remarkably high in the Seoul metropolitan area, Chungcheongbuk-do Province, southwest shore, Daegu Metropolitan City, and Jeju Island (Figs. 2 and 3). These hotspot areas for IAPs had 2.1 times more alien plants than non-hot spot areas and were explained by a combination of environmental factors (Table 1). Climate-related variables and random spatial variables were the major variables. The high strength of spatial autocorrelation implied that IAPs have not yet reached an equilibrium state and that their range is still expanding.

We included functional traits in the model to increase the explanatory power and predictive power based on the assumption that the functional traits of species can





explain the magnitude and the signs of response of the species to environmental variables. Of the total variance explained by environmental variables, 55% was accounted for by traits. Therefore, functional traits were an important predictor of the response of species to environmental factors, as we expected.

We also checked whether the importance of variables changed with family (Fig. S1). We found that major environmental variables differed slightly among families. Most of these differences seemed to be rooted in the different traits of families; therefore, we analyzed the relationship between traits and environmental factors.

The species richness of invasive alien plants was positively correlated with isothermality (bio 3), maximum temperature of the warmest month (bio 5), precipitation of the driest month (bio 14), and road density (Fig. 4). In contrast, it was negatively correlated with the seasonality of temperature (bio 4), precipitation of the warmest quarter (bio 18), and distance to rivers and the sea.

Figure 5a shows how traits affected the responses of IAPs to environmental variables when the 95% credible interval did not contain zero (level of absolute value of support ≥ 0.95 or ≤ -0.95). Species with higher SLA were associated with lower temperature seasonality (Fig. 5b). Taller species were associated with low isothermality (Fig. 5c). In contrast, seed mass traits were positively associated with the high maximum temperature of the warmest month, but exhibited a threshold-like pattern (Fig. 5d). The community weighted mean of seed mass was monotonic until the maximum temperature of the

warmest month reached 29 °C, and increased above that temperature.

Discussion

Environmental conditions under which the species richness of IAPs was high were determined by plotting estimated species richness with changes in each environmental variable. We confirmed that the species richness of IAPs had a linear relationship with the selected environmental variables.

In general, hotspots of invasive species were observed in less stressful climate conditions, where fluctuations in annual temperature were low (bio 3 and bio 4). The higher species richness of IAPs was accompanied by higher temperature in summer (bio 5), which is when plant growth peaks, and higher precipitation in winter (bio 14), which is when water stress is severe. In contrast, IAP richness tended to slightly increase when precipitation in summer (bio 18) decreased, which was attributed to rainfall being concentrated in summer in Korea, with heavy rainfall adversely affecting IAP growth.

To sum up the responses of invasive alien plants to climate variables, the hotspots of invasive plants were located in less stressful climate conditions characterized by low variability in both temperature and precipitation. This result was consistent with the ruderal and competitive strategies of IAPs (Guo et al. 2018). The increasing richness of IAPs with greater proximity to rivers

Table 1 Importance of environmental and anthropogenic variables and the variance explained by traits for each variable

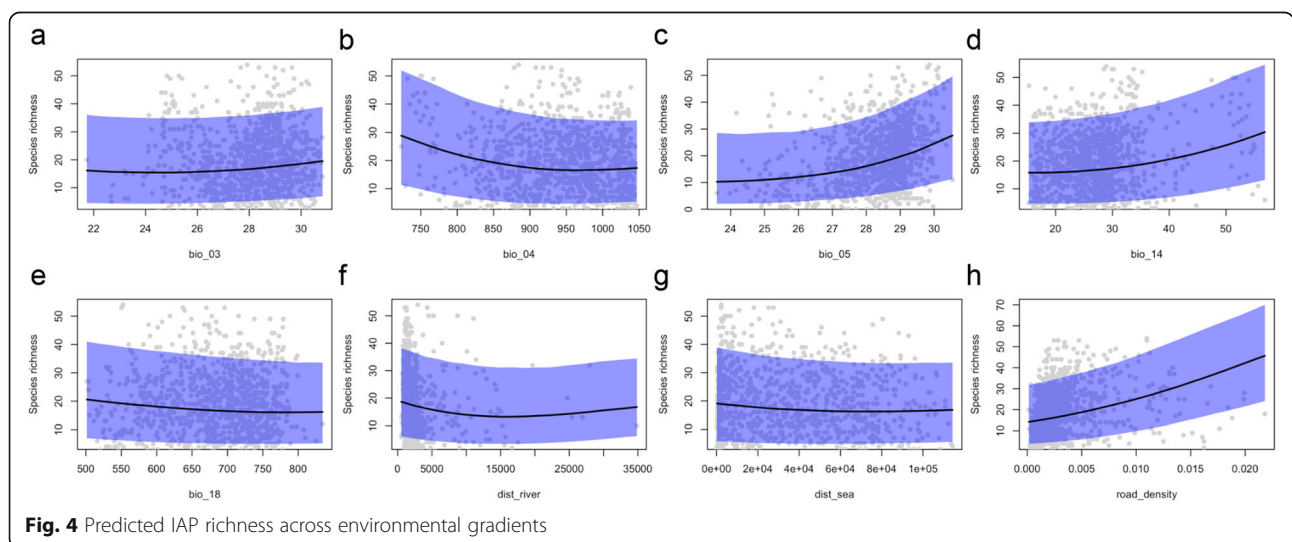
Variable	Relative importance	%Var explained by traits
Bio 3 (isothermality)	3%	44%
Bio 4 (temperature seasonality)	10%	30%
Bio 5 (max temperature of warmest month)	11%	67%
Bio 14 (precipitation of driest month)	5%	22%
Bio 18 (precipitation of warmest quarter)	3%	22%
Distance from river	4%	67%
Distance from sea	3%	29%
Road density	3%	39%
Random: sample	60%	–

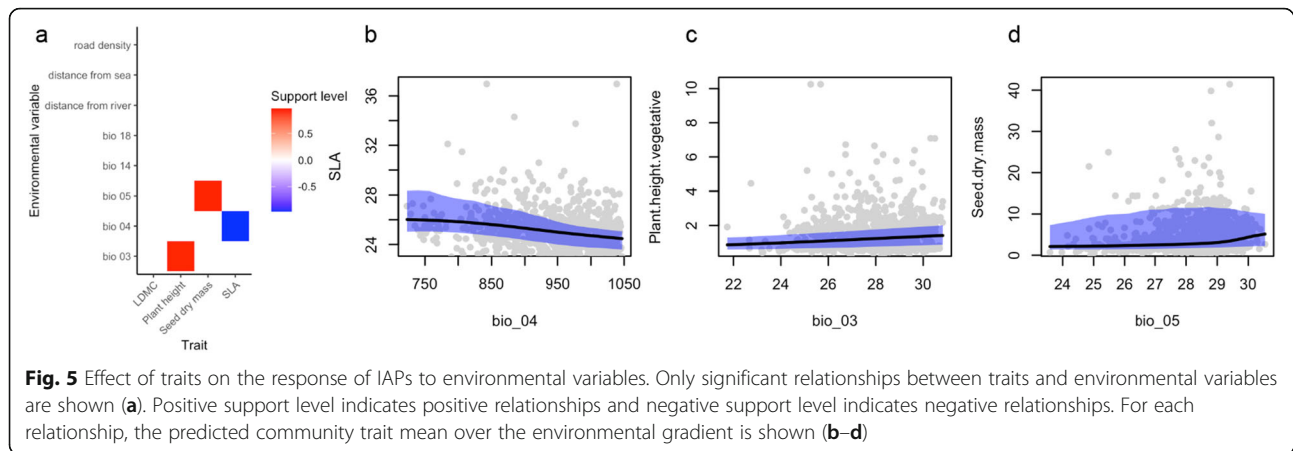
corresponded to a previously reported phenomenon that riparian wetlands are more susceptible to the invasion of alien species than other ecosystems (Pysek and Prach 1994; Hood and Naiman 2000).

Disturbances caused by anthropogenic factors and water flow positively affected hotspots. These results were consistent with previous reports on the ruderal and competitive strategies of invasive plants. Dawson et al. (2017) stated that coastal regions tend to have higher species richness at a global scale. Our study also showed that the richness of IAPs closer to the sea was higher. The presence of ports, which are typical pathways of invasion, might explain the high richness of IAPs in coastal regions (Hulme 2009; Kaluza et al. 2010). The high richness of IAPs in areas with high road density was also supported by the results of Benedetti and Morcelli (2017). This positive relationship between roads and IAPs might be attributed to roads acting as pathways for the spread of invasive species (Joly et al. 2011; Meunier and Lavoie 2012).

Functional traits are important predictors of how each taxon responds to different environments. In a single species distribution model, the functional traits of the focal species provide no surplus information; however, in community datasets, the coefficient of environmental variables can be fine-tuned by the functional traits of each taxon. Therefore, functional traits can be used to explain the distribution of all invasive species in a unified single framework. Efforts to predict the response of IAPs to the environment or their invasiveness based on their traits are ongoing; however, the context dependence characteristic of invasion has hampered predictions (Moravcová et al. 2015; Pearson et al. 2018; Novoa et al. 2020). Few studies have attempted to include functional traits in species distribution models (Regos et al. 2019; Vesik et al. 2021), with systematic studies being required to generalize the role of functional traits.

Our study showed that plants living in a stressed environment (such as a high standard deviation of temperature) tend to have a stress-tolerant strategy,





which is represented by low SLA values and long leaf lifespan (Reich et al. 1992; Reich et al. 1997). In contrast, plants living in more stable climates tend to have ruderal/competitive strategies, which are represented by high SLA values (Lambers and Poorter 1992; Reich et al. 1997) and short leaf lifespan (Grime 1994). Thus, SLA values indicate the strategy of IAPs in relation to temperature seasonality.

Moles et al. (2009) suggested that plant height and isothermality are positively correlated, with a relatively high explanatory power ($R^2 = 0.222$). Thus, when the annual temperature range becomes smaller relative to the mean diurnal range, the dominance of taller species increases in the plant community. Shorter species are associated with stressed conditions caused by large temperature fluctuations. In contrast, taller species, which are more competitive for light resources (Westoby 1998; Aan et al. 2006; Vojtech et al. 2008), are associated with more stable conditions, with low temperature fluctuations. This trade-off in investment in height documented by Falster and Westoby (2003). In other words, shorter IAPs are associated with more stressed conditions (due to greater environmental fluctuations), whereas taller IAPs are associated with less stressed conditions.

Under more stressed conditions, plants tend to have larger and heavier seeds than under more stable conditions, which is partially attributed to the positive influence of seed weight on establishment success (Harper et al. 1970; Smith and Fretwell 1974; Pluess et al. 2005). Temperature stress is one factor causing seed weight to increase. For example, Pluess et al. (2005) found that the seed weight of alpine plant species increased with increasing elevation. Both cold and heat stress can inhibit plant development, growth, and yield (Lobell and Asner 2003; Lobell and Field 2007). Our study showed that plants with heavier seed traits prevailed when the maximum temperature in summer exceeded 29 °C.

This study located the hotspots of IAPs throughout Korea, and identified relevant environmental and

anthropogenic factors. We confirmed that functional traits are relevant and important factors in determining the responses of IAPs to the environment. In the future, this fundamental research could be used to build a risk map by considering the expansion rate of IAPs and socio-environmental impact. The risk map would support the development of more efficient and practical management plans for IAPs.

Conclusions

In this study, we systematically analyzed the nationwide distribution patterns of IAPs in Korea to locate hotspots and to identify associated abiotic and/or disturbance-related factors. We also analyzed the interaction between the environment and functional traits. The predicted species richness of IAPs was high in the Seoul metropolitan area (suburbs), southwest shore, and Jeju Island. This distribution map developed here could be used to create a risk map. The hotspots of invasive plants are expected to appear in more stable climates, where fluctuations in temperature and precipitation are low. Hotspots might also be associated to high road density and proximity to rivers or the sea. Functional traits are closely related to the ecological strategies of plants, shaping how species respond to various environmental filters, with our results supporting this. In less stressed conditions, IAPs with a higher SLA and plant height prevailed. In heat stress environments, IAPs with heavier seed masses were increasingly present. These results were consistent with previous reports on ruderal and competitive strategies of invasive plants, rather than the stress-tolerant strategy. The relationship between traits and environmental factors could also be used to predict invasion success based on functional traits.

Abbreviations

IAPs: Invasive alien plants; AUC: Area under curve; JSDM: Joint species distribution model; HMSC: Hierarchical model of species communities; NNGP: Nearest neighbor Gaussian process

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s41610-021-00196-9>.

Additional file 1: Table S1. Explanatory and predictive power of the Bayesian JSDM model per species. Data were sorted in descending order of AUC predictive power. N: number of occurrences; RMSE: root mean square error; AUC: area under the curve.

Additional file 2: Fig. S1.

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Authors' contributions

MO performed the analyses and wrote the manuscript. HL conceived the study, advised the analysis, and reviewed and edited the manuscript. YH collected and cleaned the data of the alien plant list and their functional traits. E.J.L. reviewed and edited the manuscript. All authors have read and approved the final manuscript.

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Availability of data and materials

The datasets generated and/or analyzed during the current study are available from the corresponding author upon reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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