

RESEARCH ARTICLE

Distributions of non-native and native plants are not determined by the same environmental factors

Bart Steen^{1,2}  | Antoine Adde³  | Martin A. Schlaepfer⁴ | Antoine Guisan^{1,5}  | Luigi Maiorano² 

¹Institute of Earth Surface Dynamics, University of Lausanne, Lausanne, Switzerland

²Department of Biology and Biotechnology 'Charles Darwin', Sapienza University of Rome, Rome, Italy

³Swiss Federal Institute of Aquatic Science and Technology, Dübendorf, Switzerland

⁴Institute for Environmental Sciences, Université de Genève, Genève 5, Switzerland

⁵Department of Ecology and Evolution, University of Lausanne, Lausanne, Switzerland

Correspondence

Bart Steen

Email: bart.steen@unil.ch

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Abstract

1. Global environmental change will cause shifts in species communities, with non-native species likely replacing native ones at an unprecedented rate. This will have consequences for biodiversity and ecosystem services, in addition to the ecological and economic damage caused by those non-native species that are invasive. Understanding general patterns driving distributions of native and non-native species is therefore vital, but no study has compared yet whether environmental variables that correlate with a species' presence differ between the two groups other than at local scale and often with very limited sample size.
2. In this study, we focus on 141 native and non-native congeneric plant species pairs at the scale of Switzerland. In the framework of correlative species distribution models, we used newly developed methods for efficient automated selection of a parsimonious number of predictor environmental variables to determine which ones, out of a large candidate set in eight classes, have the strongest explanatory power for both species groups.
3. Our results indicated that variables influence the two groups in significantly different ways. Climate was by far the strongest determinant of both native and non-native species distributions, although it had significantly more explanatory power in native species models.
4. Models for non-native species were significantly more influenced by anthropogenic factors, land use variables and forest cover. The presence of non-native species was also associated with habitats with a significantly lower mean natural-ity value than native species.
5. These findings provide novel empirical evidence for the different environmental factors driving native and non-native plants' distributions and guidance for non-native species management.
6. Practical implications: species distribution models are an increasingly frequently advised tool for conservation management and our results provide guidelines on which covariates should be specifically considered to assess the habitat suitability

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of non-native versus native species. The distributions of the former group of species are particularly important to research, as, in time, they may turn invasive. In addition, areas close to infrastructure should be scanned regularly for incipient colonizations by non-native species, especially in as yet uninvaded areas, such as high mountains.

KEYWORDS

alien species, covariate selection, land use, naturalness, SDM, species distribution models, transportation

1 | INTRODUCTION

Understanding the environmental factors that determine a species' distribution is a foundational step in ecology (Brown et al., 1996). Species' distributions are shaped by abiotic and biotic factors and their spatio-temporal variations (Pulliam, 2000). Humans have significantly modified both the biosphere and geosphere (Steffen et al., 2018), for example by modifying land cover, altering the climate and moving species outside of their historical ranges (IPBES, 2019). This begs the question whether these factors, and which ones, shape current species distributions (Guisan et al., 2013; Thuiller et al., 2008). In this regard, the introduction of species outside of their historical ranges can be used as a large-scale 'natural experiment' to investigate what drives changes in species distributions (Colautti & Lau, 2016; Yoshida et al., 2007). It can provide insight into the different pressures that are being put on native communities, and the pressures experienced by non-native species in a new environment. In addition, it can reveal how and where populations will change in the modern, heavily globalized world. Species are labelled as *non-native* (alternatively as introduced, alien or exotic) when they have spread beyond their natural home range, that is whose colonization of new regions has been influenced by humans (Soto et al., 2024). Non-native species are further labelled as invasive if their presence is associated with clear economic losses, undesirable human health impacts (e.g. allergenicity) or are perceived to harm native biodiversity (FOEN, 2022; InfoSpecies, n.d.-a, n.d.-b; Pyšek et al., 2020).

Biologists generally study invasive species either to observe evolutionarily novel situations, or to understand how to anticipate and mitigate their undesirable effects (Guisan et al., 2014; Van Kleunen et al., 2018). The overwhelming majority of non-native species, however, are not considered invasive (European Environment Agency, 2013). For instance, they represent only 12% of non-native plant species in Switzerland (Infoflora, n.d.) and 15% of total Swiss non-native species (Infoflora, 2022). As much focus is put on the invasive fraction, less is generally known about introduced non-native species ecology (where they are established) and their functions (how they interact with other biotic and abiotic components of their ecosystem). Such questions are important both to better predict the probability of a non-native species becoming invasive but also to consider their potentially harmful effects on ecosystems or, reversely,

their potentially desirable contributions to ecosystem resilience and the contributions to human well-being (Davis et al., 2011; Sax et al., 2022). However, it is important to note that species that are invasive don't start out as such. It can take decades before a taxon displays the typical characteristics of an invasive species (Robeck et al., 2024). A species therefore is labelled as invasive only when the damage is already ongoing, and thus remediation is often the only management option on the table. Investigating whether non-native and native species share (or not) similar properties can thus be instrumental to shift from remediation to prevention, which is a preferable alternative. It is therefore important to investigate whether non-native and native species share (or not) similar properties (e.g. climatic niche, colonization capacity, ability to tolerate human disturbances; Davis et al., 2011; Pyšek et al., 2020), and to not limit ourselves to only researching non-native species that are already labelled as invasive. In this regard, species distribution models (SDMs; Guisan et al., 2017) are important tools to identify, in geographic space, relationships between species observations (presence and sometimes also absence; that is the response variable) and attributes of the abiotic environment (i.e. the covariates), such as mean annual temperature or land use types. They are popular tools in conservation planning and ecological studies (Araujo et al., 2019; Barbet-Massin et al., 2012; Guisan et al., 2013; Low et al., 2021), despite being underused in practice (Tulloch et al., 2016). By identifying key environmental factors associated with a species' distribution, SDMs can be used as explanatory tools to understand the relationship between the distributions of species and the environment, for instance to assess whether environmental drivers differ between native and non-native species.

Bioclimatic factors have a strong influence on both native and non-native species occurrence and establishment (Broennimann et al., 2021; Petitpierre et al., 2016; Zimmermann et al., 2009). In addition, many studies have established a statistical association between presence of non-native species and anthropogenic factors (Pyšek et al., 2020), including human population density, global trade network connectivity and gross domestic product (Bonnamour et al., 2021; Chapman et al., 2017; Lembrechts et al., 2017; Zhou et al., 2020). Furthermore, anthropogenically disturbed areas are more likely to be colonized by non-native species (Oshima & Takahashi, 2020; Rojas-Sandoval et al., 2024), particularly by invasive plants (Meyer et al., 2021), due to opened niches and probable

excess of nutrient availability, among other things. At a local scale, the occurrence for a non-native population is further conditioned by the presence of nearby population sources (Cook et al., 2021; Froese et al., 2019). All these latter factors, however, can also potentially determine the distribution of native species, so that it remains unclear whether similar or different environmental factors determine the distribution of native versus non-native species.

However, despite the proven effectiveness of SDMs in conservation planning (Eckert et al., 2020; Guisan et al., 2013), they suffer from a well-known potential drawback: the niche of the modelled species is assumed to be at equilibrium with the environment. This assumption is not satisfied for at least some non-native species, since their colonization of new areas is progressing and their niche is still expanding (Broennimann & Guisan, 2008; Carlin et al., 2022). The assumption may, however, hold up better for some native species (Normand et al., 2011; Steen et al., 2024). This is another reason why it is important to compare the processes driving the distributions of native and non-native species. Such changes can be analysed under the COUE (centroid shift, overlap, unfilling and expansion) framework postulated by Guisan et al. (2014). This brings us to another reason SDMs are interesting tools to study this concept: they allow for assessing whether there is niche overlap between native and introduced species. Niche overlap would imply competition, whilst niche divergence would mean possible co-existence.

Here, we take advantage of a large set of existing SDMs previously generated by a modelling pipeline that contains an automatic selection of the environmental variables (Adde, Rey, Brun, et al., 2023; Adde, Rey, Fopp, et al., 2023) to test whether the set of factors finally selected in the model differs between non-native exotic species and their native congeners. One congener was selected randomly for each exotic species. We focused on congeneric species pairs in order to mitigate as much as possible all confounding factors existing between the target native and non-native species. Using congeners, the major difference between the two species groups should be in their degree of nativeness. Other factors like differing growth speeds, different ability to generate propagules, different shade tolerance, etc. are theoretically comparable in our paired sampling design.

Specifically, we formulate and test the following hypotheses:

1. Native and non-native species' distributions are driven by different environmental factors.
2. Non-native species favour areas that are in close proximity to human infrastructures.
3. Non-native species' distributions are more strongly driven by anthropogenically altered natural environments.

2 | MATERIALS AND METHODS

Species distribution models of Swiss plant species were fit using the new N-SDM multi-species modelling software (Adde, Rey, Brun, et al., 2023) that includes an automated procedure to select the best

covariates (i.e. environmental factors) out of a panel of numerous candidate ones (Adde, Rey, Fopp, et al., 2023). Of these outputs, pairs of congeneric native and non-native species were chosen for comparative analysis and the environmental variables were divided into eight different classes (Table 1). We analysed in a paired way how often these variable classes were selected in both species groups, and for the selected variables what was their average importance. In addition, we made an ordinal measure of naturalness of land use/land cover factors and compared the naturalness scores between both species groups.

2.1 | Study area

Switzerland is home to approximately 2'800 known plant species (Lauber et al., 2018), of which 730 are considered non-native (FOEN, 2022). The country is characterized by sharp altitudinal gradients, and a large variability in climate (Petitpierre et al., 2016). Major habitats include grasslands, montane and subalpine forests (with coniferous forests spreading to higher altitudes than deciduous ones) and fully unvegetated areas at the highest elevations (Scherrer et al., 2020; Schwarz et al., 2004).

2.2 | Species distribution models

Species distribution models were previously constructed for all possible plant species in Switzerland with enough occurrence data for model fitting and using an efficient automatic selection process to identify the subset of the 833 initial environmental variables that have the strongest association with a species' presence (Adde, Rey, Fopp, et al., 2023). For each species, SDMs were fitted at two levels (continental and regional) in a nested design to prevent niche truncation (Adde, Rey, Brun, et al., 2023; Chevalier et al., 2021). At the continental level (here Europe), a bioclimatic SDM was fitted to capture the species' whole climatic niche (Chevalier et al., 2022). This output was then clipped to the regional-level extent (here Switzerland) and used it as covariate for the regional-level model, as similarly done by Chevalier et al. (2022). The continental model output (i.e. bioclimatic envelope) extracted for fitting the regional-level model was the only covariate that was always forced to be included in the final set of covariates. All other variables were candidate predictors and selected automatically using the *covsel* R package (Adde, Rey, Fopp, et al., 2023; see next section).

For the continental-level model, species observation data were retrieved from the Global Biodiversity Information Facility (GBIF; <https://doi.org/10.15468/dl.zwp3dx>; accessed on the 27th of October 2021). For the regional-level model, data from the Infospecies database (www.infospecies.ch), the Swiss centre of species information, were used. At both levels, data were retrieved for the time period of 1980–2020 and the occurrence records were spatially disaggregated using a minimal distance of 1 km between two points at the continental level and 200 m at the regional level.

Class	Examples	Level	Number of candidates
Bioclimatic envelope	Output from continental scale model	Continental	19
Edaphic	Nitrogen and phosphorus content, soil moisture variability	Regional	8
Hydrological (hydro)	Distance to lake, distance to river, slope. Baseflow index	Regional	10
Topographic (topo)	Aspect, hill shade, slope	Regional	3
Human population density (popdensity)	Humans per 25m	Regional	1
Transport	Noise pollution index, distance to road/topographic distance to road	Regional	3
Vegetation (vege)	Canopy cover, proportion of different forest types	Regional	3
Land use/land cover (LULC)	Forest, agriculture, farm pastures, scattered fruit trees	Regional	39

TABLE 1 The classes of environmental variables used to fit the SDMs at the Swiss-scale (Külling et al., 2024).

2.3 | Environmental covariates

Environmental covariates used to fit SDMs were different at each level. For the continental level, we used CHELSA version 2.1 (Karger et al., 2018) bioclimatic variables available at a resolution of 1 km². For the regional level, 67 candidate covariates were retrieved from the SWECO25 database (Külling et al., 2024).

The variables fall into eight main classes (Table 1). The full list of covariates is presented in Supporting Information (Table S2).

Edaphic factors are soil related variables, such as pH, nutrient content, moisture and aeration. They were included into the study because they strongly influence the distributions of plants species and have particularly been proven to affect alien plant abundance (Bigelow & Canham, 2002; Collette & Pither, 2015; but Ender et al., 2017). The effect may be particularly strong at our local scale with a spatial resolution of 25 × 25 m, since soil variables vary strongly over small distances. Hydrological factors relate the lake/river flow and ground water. They include factors related to river morphology, river catchment discharge, distance to water and snowmelt. They are important to consider, since some of our target species are water-dependent (see Table S4). Topographic factors are mean, median, minimum and maximum hillshade, aspect (orientation) and steepness of the slope. They are related to important determinants of habitat suitability for plants, like light availability (Charbonneau & Fahrig, 2004) and potential erosion. The latter has been proven to affect species composition in the Swiss Alps (Huck et al., 2013). Human population density is both a single variable and a class. It is the number of inhabitants per 25 m pixel; an important variable to consider, since human disturbances are strong possible drivers of non-native species distributions (Pyšek et al., 2020; Zhou et al., 2020). The different transport variables are noise pollution index, Euclidean distance to roads and topographic distance to roads (meaning the shortest topographic path). These are very important variables, as they represent the main avenues for seeds

of non-native plants to spread (Lembrechts et al., 2017; Pyšek et al., 2020), though we use noise pollution as a proxy for anthropogenic activities. Vegetation variables are: canopy cover (minimum, maximum and medium), proportion of coniferous forest and proportion of deciduous forest. These proportions are calculated using a moving window (Külling et al., 2024), the size of which can range from 25 to 5000 m and is chosen automatically based on highest explanatory power by the *covsel* R package (Adde, Rey, Fopp, et al., 2023). These moving windows were also used for the land use/land cover (LULC) class (Adde, Rey, Brun, et al., 2023). Examples of the many variables in the LULC class are devastated forest, forest fresh cuts and mountain meadows and pastures. All these environmental factors affect light conditions, which has been shown to be a strong influencing factor of alien plant abundance (Charbonneau & Fahrig, 2004). In addition, forest disturbances have been shown to be positively correlated with alien plant invasion (Oshima & Takahashi, 2020).

Automated covariate selection was done by using the *covsel* R package (Adde, Rey, Fopp, et al., 2023), whose outputs include a list of environmental variables that are statistically associated with each species' presences (across all species), a score of their relative importance in the model (Table 2). The variable that best explains each species distribution is assigned an importance value of 1, and the others are assigned the appropriate fraction. The full dataset used in this study is available online (Adde, 2024).

2.4 | Selection of species pairs

We established pairs of congeneric plant species composed of a native and a non-native to control for ecological characteristics that could be attributed to a shared evolutionary history and to obtain an equal number of units in each group. First, we identified non-native species with at least one native congener. A random draw (function 'sample' in R) selected only one native species in cases where

TABLE 2 Covariates selected for the species pairs *Bidens cernua* (native) and *Bidens frondosa* (non-native), *Heracleum mantegazzianum* (non-native) and *Heracleum sphondylium*, (native), *Vinca major* (non-native) and *Vinca minor* (native) their average importance and the naturality score of the selected variables belonging to the LULC class.

Species modelled	Variables selected	Average variable importance	Naturality score of LULC variables
<i>Bidens cernua</i>	Bioclimatic envelope	0.96	
	Distance to lake	0.46	
	Settlement urban amenities cover	0.32	1
	Alpine pastures cover	0.31	4
	Soil moisture	0.28	
	Slope	0.24	
	Soil ph	0.2	
<i>Bidens frondosa</i>	Bioclimatic envelope	1.00	
	Agriculture cover	0.19	2
	Settlement urban amenities cover	0.18	1
	Other arable land and meadows cover	0.18	3
	Soil moisture	0.11	
	Soil aeration	0.11	
	Unproductive grass and shrubs cover	0.09	4
	Euclidean distance to road	0.07	
<i>Heracleum mantegazzianum</i>	Bioclimatic envelope	1.00	
	Euclidean distance to road	0.22	
	Favourable arable land and meadows cover	0.19	3
	Grassland meadows cover	0.16	3
	Soil moisture	0.14	
	Deciduous forest cover	0.13	
	Alpine pastures cover	0.13	4
	Path distance to road	0.08	
	Other arable land and meadows cover	0.07	3
	Distance to lake	0.04	
	Wetlands cover	0.03	
	Remote and steep alpine meadows and pastures cover	0.02	4
<i>Heracleum sphondylium</i>	Bioclimatic envelope	1.00	
	Soil nutrients	0.25	
	Soil moisture variability	0.20	
	Hillshade	0.20	
	Slope	0.15	
	Soil ph	0.12	
	Distance to river	0.11	
	Soil humus	0.10	
	Brush forest cover	0.09	5
	Soil moisture	0.08	
	Deciduous forest cover	0.08	
	Clusters of trees cover	0.03	3
	<i>Vinca minor</i>	Bioclimatic envelope	1.00
Other arable land and meadows cover		0.29	3
Soil aeration		0.27	
Soil ph		0.26	

(Continues)

TABLE 2 (Continued)

Species modelled	Variables selected	Average variable importance	Naturality score of LULC variables
	Canopy height	0.24	
	Euclidean distance to road	0.21	
	Agriculture cover	0.12	2
	Intensive agriculture cover	0.10	2
<i>Vinca major</i>	Bioclimatic envelope	0.96	
	Euclidean distance to road	0.35	
	Soil humus	0.21	
	Agriculture cover	0.15	2
	Coniferous forest cover	0.14	
	Deciduous forest cover	0.11	
	Forest cover	0.09	5
	Settlement urban amenities cover	0.09	1
	Soil ph	0.07	
	Noise pollution index	0.05	
	Open forest cover	0.03	5

Naturality score	Definition	Example
1	Very heavily modified	Impermeable surfaces, such as asphalt or concrete roads, mineral roof tops, artificial turf (sports field)
2	Heavily modified	Permeable surfaces, such as roads and parking lots made of gravel and dirt; intensive agriculture with tilling and use of herbicides and pesticides
3	Moderately modified	Semi-natural habit, such as agro-forestry, urban parks with abundant vegetation and water, gardens, green roofs, cemeteries
4	Lightly modified	Areas with low density of trails, roads and buildings or managed for nature-oriented goals such cultural and regulating ecosystem services or biodiversity targets
5	Very lightly or not modified	Areas considered 'wild' or lightly managed for unique biodiversity (high species richness, rare and endemic species)

TABLE 3 Ordinal classification of naturality score of the land use/land cover variables. 1 is the highest degree of anthropogenic interference, that is the least natural and 5 is the lowest degree of anthropogenic interference. Derived from (Brown & Vivas, 2005; Kowarik, 1988, 1995; Radford et al., 2019).

multiple native congeners existed. This resulted in 141 native–non-native species pairs, of which 15 (11%) are invasive, a percentage similar to the ratio in all non-native plant species in Switzerland (12%) (Inflorella, n.d.).

2.5 | Comparing SDM predictor variables between native and non-native plant species

Two approaches were used to compare the environmental requirements of native versus non-native species. First, we tested within each class of variables for differences in the variables automatically selected in the models of the two groups. We analysed what class the selected variables belonged to and their relative importance (Smith & Santos, 2020). In the cases where covariates of a specific environmental variable class were only selected in one

of the two congeners in a pair, the pair was dropped from that particular analysis. This was necessary to keep our paired samples design. The 'var.test' function in R was used to verify equality of variances and based on this result, the comparison between pairs was done using the 't.test' function in R, with either equal or unequal variances.

We investigated the three vegetation variables (minimum/maximum/medium canopy cover, proportion of coniferous forest and proportion of deciduous forest) more closely, by analysing how often they were selected as a covariate and what their average variable importances were for native and non-native species.

A second analysis was devised to test for an association with anthropogenic habitats. Each land use/land cover (LULC) class was assigned an ordinal naturality score. Naturality captures the extent to which a habitat has been modified by human activity. Our definition for each ordinal value (Table 3) and the specific scores

attributed to each habitat category (Table S3) is based on similar attempts in prior studies (Brown & Vivas, 2005; Kowarik, 1988, 1995; Radford et al., 2019).

For each SDM, the naturality value was calculated as the mean of all significant LULC categories times their respective naturality scores. Naturality values across species groups were compared with a paired t-test, as with other environmental variables.

As the naturality score of a habitat type likely reflects human activity at least at a coarse scale and given that the naturality score was established independently of the modelled presence of non-native species, we assumed that the numerical values could be used for testing differences between groups of species.

In order to make our results easier to interpret considering the ecology of the species, we split up our non-native species into several categories considering different characteristics. In particular, we considered invasiveness, degree of naturalization in Switzerland (introduced more or less than 40 years ago), region of origin, growth form according to Raunkiaer (1977), and habitat that the species are bound to (according to InfoSpecies, n.d.-b).

We tested the significance of the differences in AUC values for each subdivision using a t-test.

3 | RESULTS

Species distribution models were fitted for 141 non-native plant species that had at least one native and likewise modelled congener (i.e. native species within the same genus; see Table S1). The number of covariates in each SDM ranged between 5 and 12. Example SDM outputs from a species pair are provided in the Supporting Information, Figure S1.

After eliminating species pairs in which only one congeneric selected a variable in the class of interest, we had the following numbers of species pairs per class: 141 for the bioclimatic envelope (since it was forced into each model to avoid niche truncation), 139 for land use/land cover variables, 96 for edaphic variables, 53 for transportation variables, 50 for topographic variables, 41 for vegetation variables and 24 for hydrological variables.

Overall, bioclimatic factors had by far the highest variable importance in both species groups (Figure 1). The bioclimatic envelope, that is the output of the European-scale model based on bioclimatic variables only, was significantly more important for native species (paired t-test: $p=0.009$, Figure 1). Predictor variables from other classes were less important (i.e. had lower significance scores) but could be significantly associated with the distribution of at least some species (both native and non-native). Three classes of predictor variables have significantly greater average importance in non-native species than in native species models: transportation, vegetation and land use/cover (paired t-tests: $p=0.018$, $p=0.007$, $p=0.007$, respectively; Figure 1), though no noticeable difference in the frequency of selection of these variable groups between native and non-native SDMs could be found (Table S5).

We found no significant differences between native and non-native species models for topographic or water-related factors (t-tests: $p=0.055$, $p=0.716$, respectively, Figure 1). No model selected human population density as predictor. However, some models did select proxies for human population density, like the transport variables (Figure 1).

There are only a few variables in vegetation and transportation-based classes. This allows us to use our pairwise analyses to further investigate these variables. The other classes have too many variables and would lead to too many species pairs being eliminated. Even with the topographic distance to roads variable, there were only two species pairs that included the variable (see Figure 2). For the same reason, we had to consider the three canopy cover variables as only one. The only variables that had significantly higher variable importance in one class were the proportion of deciduous and coniferous forest, with a higher average for non-native species (see Figure 2).

Finally, the average naturality scores of land use/cover variables were significantly higher in native species models (t-test, $p=2.03 \times 10^{-5}$, see Figure 3).

When dividing the non-native species into invasive and non-invasive species, we found that barring climate, which was of course the most important variable everywhere, edaphic and vegetation factors were the most important for invasive species, but

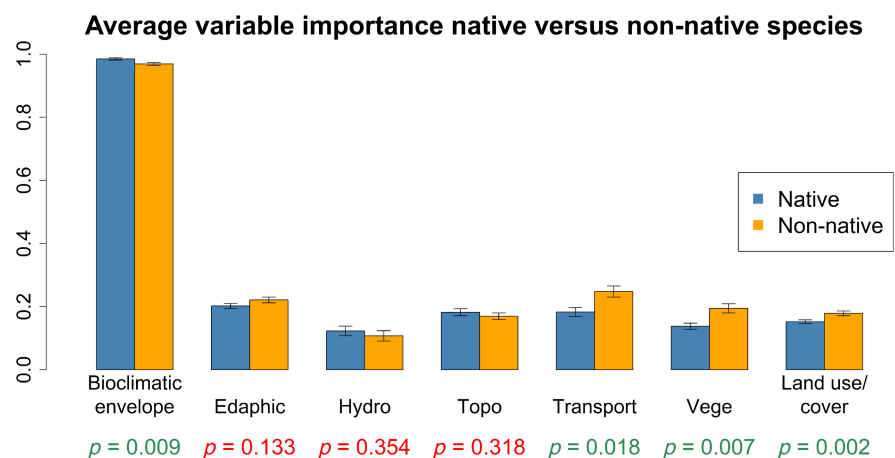


FIGURE 1 Comparison of average importance of variable classes selected by models built for native species versus models built for non-native species and p-values of paired t-tests. Green values indicate significant differences, red values indicate non-significant differences.

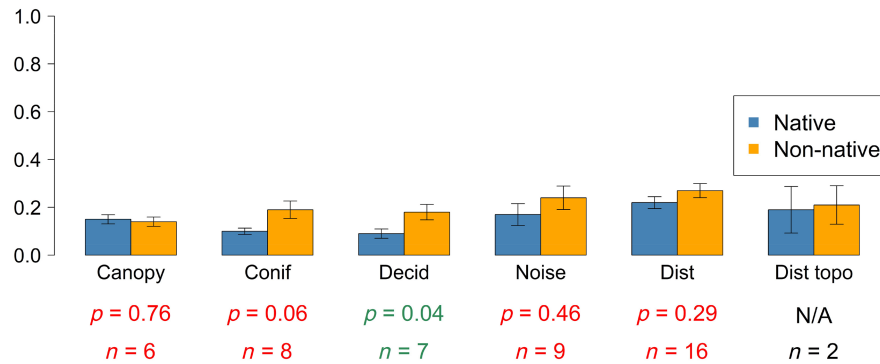


FIGURE 2 Average variable importance of the three vegetation-based factors and the three transport based factors by both native and non-native models, plus respective sample sizes, with paired t-tests for sample differences. Canopy, percentage of canopy cover; Conif, proportion of coniferous forest; Decid, Proportion of deciduous forest; Noise, noise pollution index; Dist, Euclidian distance to road; Dist topo, topographic distance to road. Green values indicate significant differences, red values indicate non-significant differences.

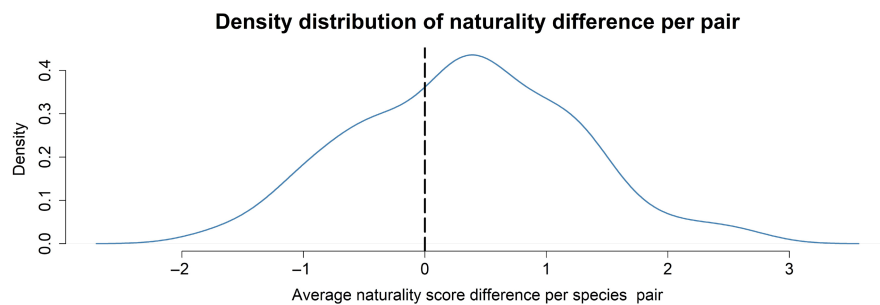


FIGURE 3 Kernel density distribution of average naturality score of LULC variables per species pair. Calculated by subtracting the average naturality score of the non-native species from that of their matching native congeners. The average naturality score was 3.10 for native species and 2.77 for non-native species, which was significantly different (paired t-test: $p = 2.03 \times 10^{-5}$).

no significant differences were found between the variable importances of these latter factors. For non-native species, transportation variables had the highest variable importance, again after climate.

When splitting the non-native species into the taxa that have been in Switzerland for over 40 years and the ones that were not, we found that in both cases transportation variables had the most powerful predictors after climate, and the importance was significantly higher for the more recent species (non-paired t-test: $p = 0.04381$).

We found that vegetation factors had on average the highest variable importance of all groups of environmental factors in models of non-native species from Asia (again after climate). The difference with the second most important variable group, transportation factors, was not found to be significant ($p = 0.5511$). For all species from South America, edaphic variables have the highest predictive power (with topographic next and transportation third; again, after climate). For species from all the other continents (excluding the ones with fewer than 6 species), including Europe itself, the transportation variables had the highest predictive power after climate, but the difference with it and the second most important variable group was never significant.

When analysing variable importance in different growth forms, we find the same pattern for chamaephytes, phanerophytes, hemicryptophytes and therophytes: after climate, transportation variable

importance is highest; however, it is not significantly higher than other important variables. This is likely a consequence of too low sample size. However, we did find two growth forms that showed a different pattern: For geophytes, the edaphic variables were the most potent predictors, then vegetation variables and finally transportation variables. Again, no significant difference was found between these variable groups. Finally, when putting all woody plants together (woody chamaephytes + phanerophytes), vegetation variables were most important, with transportation variables second (but there was again no significant difference).

Splitting up the non-native species that are bound to certain habitats (76 total) revealed that 40 of them occur in (and many are common or dominant in) pioneer vegetation of human-disturbed areas. It was the largest group. Second largest was plantations, fields and crops (16 total) and third were heaths, margins and meadows (12 total).

4 | DISCUSSION

Our results show that, overall, the environmental factors that determine the distribution of both native and non-native species are largely similar, yet with interesting differences. Hypothesis 1 (the distributions of native and non-native plants are determined by

different environmental factors) is therefore partly confirmed. In fact, the distribution of species from both groups are correlated first and foremost with bioclimatic factors, suggesting that climatic factors represent a key filter in determining where species are established. However, bioclimatic factors appear slightly less important in non-native species. The significantly higher importance of the bioclimatic envelope for native species (meaning the output of the Europe-scale model of the species, which was constructed using only bioclimatic variables) is what is expected from species that are more likely to be at equilibrium with the environment (Early & Sax, 2014; Guisan et al., 2014; Perret et al., 2019). The most likely explanation is that some non-native species are still expanding their range and may not yet have occupied their entire realized niche in the new ranges (i.e. 'unfilling' in the COUE framework; Guisan et al., 2014). Anyway, climate matching was still shown to be an important factor for non-native species (e.g. Broennimann et al., 2021 for mammals, Petitpierre et al., 2012 for plants).

Hypothesis 2 (non-native species distributions are more strongly associated with areas close to human infrastructure than native species distributions) is fully confirmed. Variables associated with transportation (e.g. proximity to roads, LULC categories and vegetation; e.g. extent of deciduous canopy cover within a given radius of the species' observation) indeed are correlated with non-native species' distributions more than native species' distributions. This seems to indicate that factors that are not under the influence of human activities (soil characteristics, topography, hydrological characteristics) affect native and non-native species distributions equally and that, by contrast, environmental variables shaped by anthropogenic activities are more likely to be associated with the presence of non-native species. This is consistent with literature on the distribution of non-native species (Essl et al., 2015; Pyšek et al., 2020). Firstly, human transportation plays a great role in the dispersal of non-native species. There are many examples of non-native and invasive species spreading via ship, airplane, train or motorway (Bertelsmeier et al., 2017; Essl et al., 2015; Mang et al., 2018). This may also explain why human population density was never chosen as a predictor in any model, whilst the transportation variables (distance to roads and noise pollution index) were. This implies that human density itself is a less powerful predictor, which seems logical, since non-native species are often spread by human movement (Capinha et al., 2015). The importance of transportation variables is largely reflected when subdividing the target species by region of origin; species from Europe, North America and Africa all favoured transportation variables (though no significant differences were found with other variable groups). Species of Asian origin, conversely, favoured vegetation variables more, indicating that these species have already spread beyond the proximity of human infrastructure.

The observation that anthropogenic variables more strongly predict non-native species distributions also conforms to the propagule pressure hypothesis cluster, which is one of the five major ones synthesized by Enders et al. (2020) on what can make non-native species invasive (see also Pyšek et al., 2010). Many of the hypotheses presented by Enders et al. focus on what drives non-native species

success and probability of establishment and are therefore relevant to be considered here.

The propagule pressure cluster centres around the idea that the more individuals of a non-native species arrive in a new place, the higher the chance that the species will establish itself.

The naturality values of LULC categories in SDMs of non-native species were, on average, 0.3 lower than LULC categories SDMs of native species. This is supported by the fact that the majority of non-native species were bound to pioneer vegetations in human-disturbed areas and that the second most represented habitat among them is plantations, fields and crops. These results are consistent with the human commensalism hypothesis (Jeschke & Strayer, 2006), which posits a positive association between non-native species with human activities. It also concurs with several case studies on the habitat preferences of invasive species (Steen et al., 2019), with terrestrial invasive plants in particular favouring abandoned agricultural ground (Kuhman et al., 2010, 2011).

The breakdown of the non-native species highlighted the effect of naturalization: variables relating to transportation have significantly more predictive power in species that have been in Switzerland for less than 40 years. This may indicate that whilst niche shifts often happen during colonizations (Broennimann et al., 2007; Carlin et al., 2022), eventually, non-native species move closer to equilibrium with the environment. It might likewise mean that the inherent assumption of SDMs that rely on this equilibrium becomes more justified, the longer a non-native species is resident in a certain range.

This might underline the importance of managing invasive species along human infrastructure; however, in our study, we found that invasive species distributions were more powerfully predicted by edaphic and vegetation-related factors. This may be because our sample size for these species was too small (15 total), but a more likely explanation is that these have long been naturalized; all but two of the species have been in Switzerland for longer than 40 years. As a result, they have already distributed themselves beyond the proximity of human infrastructure.

Whilst no significant differences could be found when analysing variable importance within growth forms, the fact that geophytes and woody plant species show different patterns from anything else is interesting. Geophytes store nutrients and water into subterranean parts (bulbs/corms/rhizomes/tubers; Encyclopedia Britannica|Britannica, n.d.), and therefore, the soil factors are logically powerful predictors. Woody plants are strongly associated with vegetation variables, which include proportion of forests, which is their habitat. Again, it might indicate non-native species' predilection to colonize, as the proportion of forests is indicative of how many edges there are and thus of gap dynamics.

Hypothesis 3 was also confirmed. Indeed, our results show that although overall the same type of variables predict the spatial distribution of both native and non-native plants in Switzerland, small yet significant differences between groups exist in the environmental factors that appear in the SDMs. Specifically, several lines of evidence suggest that non-native species are more likely to occupy

habitat types that have been altered by human activities, which is again in agreement with the propagule pressure hypothesis cluster.

The significantly higher average importance of deciduous forest cover variables in non-native species SDMs (proportion of coniferous forest and proportion of deciduous forest; see Figure 2) may be caused by the fact that many non-native species favour gaps in the canopy and the proportion of forest cover in a certain area may be a proxy of the number of edges, which are easier to colonize (Komarul Huda et al., 2022). This is supported by the significantly higher average variable importance of the proportion of deciduous forest in non-native species models (Figure 2). A possible reason why this pattern is not observed for coniferous forests is that, in Switzerland, these tend to occur at higher altitudes than deciduous forests (Scherrer et al., 2020) and may therefore not have been colonized by non-native species to the same degree yet.

In addition, land use/cover might also reflect the non-native species colonization dynamics. Some of the many variables in this class are devastated forest, forest fresh cuts and mountain meadows and pastures.

In short, our results show that anthropogenic factors play a more important role in explaining the distributions of non-native species than those of native species, though the general patterns are rather similar for both species groups. We see that the bioclimatic variables are by far the most important explanatory variables for both native and non-native species groups.

Interesting new research questions arise from these results. For instance, do invasive non-native species favour different variables than their non-invasive counterparts? The sample size in this study was likely insufficient to accurately make this assessment. In addition, the probability of successful establishment of non-native species could be researched. For instance, Broennimann et al. (2021) have shown that the similarity of the climatic niche between the native and non-native range of a species significantly influences invasion success. Such findings could provide more insight in distribution patterns of non-native species and guide conservation actions more effectively.

Furthermore, the COUE framework could be adapted to congeneric species pairs in order to add perspective on niche comparison analysis. SDMs rely on niche conservation between native and non-native range (Guisan et al., 2014). This could lead to interesting conclusions. For instance, if the niches in native and non-native range largely overlap, SDM predictions can effectively encapsulate potential distributions of non-native species. Conversely, if the niches shift (as they have been shown to do), patterns in such a shift should be identified. Our pairwise comparison of congeners is a first step in this direction and could be supported by quantifying the degree in niche similarity resulting from species distribution maps, as was for example done by Warren et al. (2008).

From a more practical perspective, our results also show that different sets of environmental predictors could be used for modelling the distribution of non-native versus native species for practical applications (e.g. pre- and post-border evaluation of invasions; Gallien et al., 2012; Pheloung et al., 1999; Shackleton et al., 2020).

In particular, it would seem prudent to use transportation-related variables and ones with a low naturalness score/high degree of disturbance to build SDMs for non-native species, even if the latter have not (yet) become invasive. Conversely, native species could be best modelled using covariates representing relatively undisturbed habitat and climatic preferences. It must also be noted that the climate covariates must be used at the appropriate scale, as niche truncation must be avoided. This has great implications for management, since SDMs are increasingly frequently advised method for planning conservation measures (Araujo et al., 2019; Barbet-Massin et al., 2012; Guisan et al., 2013; Low et al., 2021; Tulloch et al., 2016).

Another important implication for practitioners would be aimed at foreseeing the impacts of non-native species, whether positive or negative, originating in proximity to human infrastructure. These areas would have to be scanned for incipient or ongoing colonization by non-native species and the identified taxa should be researched on their invasiveness recorded in different parts of the world. Such efforts are already ongoing in Switzerland (www.infospecies.ch) and in the EU (EASIN—European Alien Species Information Network, n.d.). In addition to scanning, the trends of the populations should be monitored, especially for strong declines or growth. This approach would be most critical to apply in the areas that have not yet been overly exposed to non-native species colonization, such as (high) mountains. Our results show that as human infrastructure expands, non-native species will probably follow. There, it would be especially important to detect colonization by non-native species early.

Finally, a word of caution to practitioners. Previous studies have shown that a correlation exists between habitat suitability (as calculated by SDMs) and species abundance/population density (Weber et al., 2017; but see Brambilla et al., 2024; Monnier-Corbel et al., 2023). This work, however, suggests that population densities of non-native species near roads and in disturbed areas should not be extrapolated to other habitat types, as there, the densities are expected to be lower.

AUTHOR CONTRIBUTIONS

Martin A. Schlaepfer and Antoine Guisan conceived the ideas, designed methodology and edited the manuscript; Luigi Maiorano designed methodology and edited the manuscript; Antoine Adde collected the data and edited the manuscript; Bart Steen analysed the data; Bart Steen led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

CONFLICT OF INTEREST STATEMENT

No conflicts of interest are known to the authors.

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DATA AVAILABILITY STATEMENT

Covariate selection data used in our study are available at <https://doi.org/10.5281/zenodo.13325636>, (Adde, 2024).

ORCID

Bart Steen  <https://orcid.org/0000-0002-2217-9510>

Antoine Adde  <https://orcid.org/0000-0003-4388-0880>

Antoine Guisan  <https://orcid.org/0000-0002-3998-4815>

Luigi Maiorano  <https://orcid.org/0000-0002-2957-8979>

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SUPPORTING INFORMATION

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

Figure S1. Example output Species Distribution Model from a species pair, for the native -nonnative species pairs *Bidens cernua* and *Bidens frondosa*, *Heracleum sphondylium* and *Heracleum mantegazzianum* and finally *Vinca minor* and *Vinca major*.

Table S1. List of target species: non-native and native congeneric species pairs.

Table S2. Full list of environmental variables (Külling et al. (in review)) used to fit models in the N-SDM pipeline.

Table S3. All land use/land cover variables and their associated naturalness score.

Table S4. List of target species and subdivision by growth form, year of introduction to Switzerland, and origin region.

Table S5. Frequency of selection of the three vegetation-based covariates and three transportation covariates by both native and non-native models.

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