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Research

Island properties dominate species traits in determining plant colonizations in an archipelago system

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The extrinsic determinants hypothesis emphasizes the essential role of environmental heterogeneity in species' colonization. Consequently, high resident species diversity can increase community susceptibility to colonizations because good habitats may support more species that are functionally similar to colonizers. On the other hand, colonization success is also likely to depend on species traits. We tested the relative importance of environmental characteristics and species traits in determining colonization success using census data of 587 vascular plant species collected about 70 yr apart from 471 islands in the archipelago of SW Finland. More specifically, we explored potential new colonization as a function of island properties (e.g. location, area, habitat diversity, number of resident species per unit area), species traits (e.g. plant height, life-form, dispersal vector, Ellenberg indicator values, association with human impact), and species' historical distributions (number of inhabited islands, nearest occurrence). Island properties and species' historical distributions were more effective than plant traits in explaining colonization outcomes. Contrary to the extrinsic determinants hypothesis, colonization success was neither associated with resident species diversity nor habitat diversity per se, although colonization was lowest on sparsely vegetated islands. Our findings lead us to propose that while plant traits related to dispersal and establishment may enhance colonization, predictions of plant colonizations primarily require understanding of habitat properties and species' historical distributions.

Keywords: colonization, community properties, functional traits, insular ecology, islands, species diversity

Introduction

Global environmental change due to habitat degradation and alterations in climate has led many species to shift their ranges and colonize new habitats (Parmesan and Yohe 2003, Hickling et al. 2006, Freeman et al. 2018). However, for sessile organisms, such as plants, colonization events may be less frequent than for species with high dispersal capacity (Walther et al. 2002). Understanding the mechanisms that promote successful plant colonization is thus essential for predicting future changes in plant communities.



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The extrinsic determinants hypothesis emphasizes the importance of environmental factors and habitat quality to species' colonization success (Naeem et al. 2000). For example, increased environmental heterogeneity (e.g. differences in grazing intensity or nutrient levels) can lead to a positive diversity–colonization relationship (Naeem et al. 2000, Davies et al. 2005). Indeed, environmental characteristics, such as the diversity of microhabitats and habitat connectivity, have been reported to enhance colonization success at a landscape scale (Auffret et al. 2017). Consequently, in broader-scale studies spanning several square kilometres, environmental factors are likely to be more important in determining species' colonization success than competition-driven biotic interactions that tend to dominate in smaller-scale studies (reviewed by Fridley et al. 2007, Smith and Côté 2019).

In addition to environmental characteristics, colonization success greatly depends on dispersal and establishment (Honnay et al. 2002, Brunet 2007, Theoharides and Duker 2007). For this reason, plant traits related to dispersal, growth and reproduction are likely to be important. As an example, tall species generally disperse further than short species (Thomson et al. 2011), and establishment increases with increasing seed mass (Kempel et al. 2013) as well as with the number of propagules (i.e. propagule pressure) (Colautti et al. 2006, Kempel et al. 2013). Moreover, leaf size and specific leaf area (SLA) are associated with competitive ability, with large- and thin-leaved species having a higher growth rate and better competitive ability than species with small and needle-like leaves (Westoby 1998). We might thus expect large-leaved species to be more successful colonizers than small-leaved species in existing plant communities. Given previous reports that more diverse communities may support greater trait diversity (Díaz and Cabido 2001, but see Mayfield et al. 2010), resident and colonizing species might share many functional traits. The presence of species with similar traits in a community also indicates that the receiving community has the abiotic conditions required by new colonizing species (Proches et al. 2008).

While manipulative experiments can reveal the causative factors behind species' colonization success, they are rarely feasible at larger spatial and temporal scales. As monitoring studies may not be sufficiently extensive, the relative importance of environmental characteristics and species traits in plant colonization at a landscape scale is largely undecided, despite decades of scientific interest (Naeem et al. 2000, Richardson and Pysek 2006, Burns 2016). In this large-scale study, we examine the relative roles of environmental characteristics and species traits in determining colonization success. We analyze the colonization success of 587 vascular plant species on 471 islands in the archipelago of SW Finland using extensive inventories conducted about 70 yr apart. We focus on the potential colonization of islands by common species that were not present in the first inventory (the 1930s) and attempt to explain colonization success recorded in the second inventory (1996–2017) using island

properties, species traits and species' historical distributions. During the observation period, larger islands have undergone grazing abandonment (von Numers and Korvenpää 2007) and the study area has experienced a slight increase in the atmospheric input of nitrogen (Hongisto and Joffe 2005), but has otherwise remained unchanged. Specifically, we tested the extrinsic determinants hypothesis (Naeem et al. 2000), which emphasizes the importance of extrinsic factors and predicts that plant colonization success increases with an increasing number of resident species (i.e. 'good' habitats support more species) that are functionally similar to the colonizers (i.e. similar species occupy similar habitats). Moreover, we hypothesized that other island properties (e.g. island area, number of habitats, proximity to a historically inhabited island) and certain plant traits (e.g. high seed number, large specific leaf area, plant height) would be positively associated with colonization success.

Material and methods

Study area

The archipelago of SW Finland covers a shallow non-tidal area in the Baltic Sea and includes at least 22 000 islands, ranging in size from a few square meters to inhabited islands with areas of tens of square kilometers (Granö et al. 1999). This mosaic structure creates a wide range of conditions and habitats on the islands throughout the archipelago. The climate is maritime, but the early part of the growing season often has continental characteristics, with low precipitation and higher insolation compared to the mainland (Anonymous 1989). The water is brackish (salinity 5–6‰; Suominen et al. 2010) and usually covered with ice during the winter. The islands emerged from the sea after the last glaciation ended ca 12 000 yr ago, and isostatic rebound continues at the rate of ca 4 mm yr⁻¹. A detailed description of the study area is provided in von Numers and van der Maarel (1998) and von Numers (2011, 2015, 2017).

The species occurrence dataset consists of paired historical and recent inventories of all vascular plants on 471 islands, which ranged from 369.2 m² to 1.73 km² in area. Most plant species were native common species or archaeophytes. The study area extends about 100 km in the S–N direction and 80 km in the W–E direction (Fig. 1). The majority of the historical inventories were conducted by Eklund (1958) between 1925 and 1946, mainly in the 1930s (447 islands), and to lesser extent by other researchers in the 1940s (Skult 1960, 23 islands) and 1964 (one island, Vaahtoranta 1964). The recent inventories were conducted between 1996 and 2017 with the most intensive effort in 1998–2010. In both inventories, species lists were compiled for each island, but no data on abundance were collected.

In the recent inventory, the islands were surveyed during the same part of the growing season as in the historical inventories; usually between 10 June and 30 July. A small

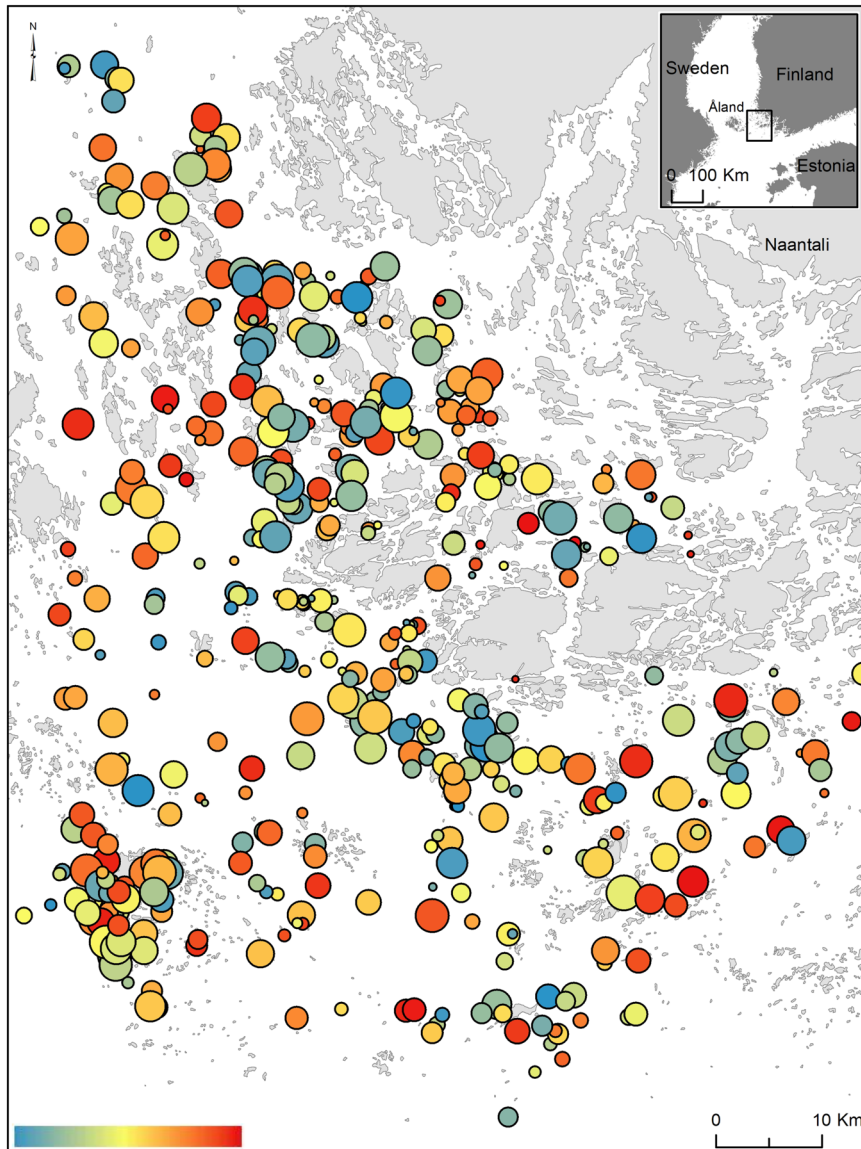


Figure 1. Map of the study archipelago, located between the Åland islands and the SW coast of mainland Finland. Surveyed islands are marked with circles ($n=471$), where size represents the relative area of the study island, and color represents invasibility, measured as the magnitude of the random effect of the colonization model. Red shades indicate a positive random effect and larger number of successful colonizers, while blue shades indicate a negative random effect and fewer colonizations.

motorboat was used for the excursions. We surveyed the islands systematically and thoroughly throughout their entire area usually beginning with the shore zone. Some islands were surveyed twice and some of the largest islands demanded several days of work. In the field, we used a species checklist with potentially occurring species on the islands following the same procedure as in the historical survey (Eklund 1958, Skult 1960). There is naturally no way to test the accuracy of the historical species lists, but they are most likely highly reliable because both Eklund and Skult were experienced botanists (Eklund devoted his life for surveying the flora of the archipelago of SW Finland). While both the historical and current inventories were conducted systematically by field

botanists, it is possible that some species remained undetected. However, this may have happened for only a few species (see von Numers and Korvenpää 2007 for examples and discussion) and we do not consider this a substantial issue in the present study.

Island properties

For each island, we recorded the number of species from the historical inventory (i.e. ‘residents’) and scaled it to island area as a measure of habitat quality and the competitive intensity that a new species would have encountered as a potential colonizer on that island. We further characterized each island

by its surface area and convolution of the shoreline (measured as the length of the shoreline divided by the circumference of a circular island with the same surface area). ArcGIS (ver. 10.1) was used to measure island area and shoreline length based on the data from the National Land Survey of Finland. We also quantified the land area within 2-km and 5-km buffer zones of each island, as these metrics, along with the distance from the nearest surveyed island inhabited by each species, provided measures of connectivity between islands. Information on occurrences of limestone was obtained from Eklund (1958). We included the coordinates (EUREF-FIN) of the island centre points as explanatory variables to detect broad spatial patterns in colonization across the study area.

The remaining island properties (see below and Table 1 for a complete list) were based on the CORINE Land Cover 2006 dataset that provides information on Finnish land cover and land use in 2006. This dataset was produced by the Finnish Environment Institute (SYKE) and is based on the automated interpretation of satellite images. We calculated the number of habitats (Num habitats and Habitat per area in Table 1) and Shannon's and Simpson's diversity indices for habitat proportions for each island using the number of

CORINE level 4 land cover classes. Islands with high habitat diversity support more species (Hannus and von Numers 2008) and we therefore expected habitat diversity to increase opportunities for colonization. We used habitat percentages rather than map cell counts to ensure our metrics of habitat occurrence were independent of island area. Habitat proportions of the CORINE level 4 were pooled into the following larger groups, which we used as separate explanatory variables (percentages given for the whole study area): open rock and bare ground (41.45%), scrub (23.29%), coniferous forest (21.32%), mixed forest (5.58%), meadow and pastures (4.39%), deciduous forest (1.79%), sand (1.29%), buildings (0.69%), shore meadow (0.13%) and marsh (0.06%). Moreover, we used the CORINE data to model the habitat dissimilarity between historically inhabited and potentially newly colonized islands by comparing the proportions of different CORINE classes. We achieved this by calculating for each species a habitat spectrum as the mean proportion of each habitat across the historically occupied islands. We then calculated the Euclidean distance between a species' habitat spectrum and habitat proportions on each uncolonized island.

Table 1. Island properties and source (CORINE=Corine Land Cover). Listed are the island properties that were used in the full model, as well as those rejected due to collinearity. All variables except limestone are on a numerical scale.

Name	Description	Source
Island properties included in the full model		
Residents per area log	Number of species in the first inventory divided by island area (log transformed)	This study
Area log	Island area (log transformed)	Map
Euref X and Y	Island centre point coordinates (EUREF-FIN).	Map
Convolution	Island perimeter divided by the perimeter of a circle of equal area	Map
Buffer 2 km log	Area of land within a 2-km buffer around the island (log transformed)	Map
Buffer 5 km log	Area of land within a 5-km buffer around the island (log transformed)	Map
Dist to historical log	Distance from the target island to the nearest surveyed island historically inhabited by the focal species (log transformed)	This study
Habitat proportions: – Buildings – Meadow or pasture – Deciduous forest – Coniferous forest – Mixed forest – Scrub – Sand – Open rock or bare ground – Marsh – Shore meadow	Proportion of Corine Land Cover types on each island	This study (CORINE)
Limestone	Presence of limestone: yes/no	Eklund 1958
Shannon habitats	Shannon diversity of habitats	This study (CORINE)
Island properties rejected from the full model due to collinearity (VIF > 5)		
Simpson habitats	Simpson diversity of habitats	This study (CORINE)
Num habitats	Number of habitats	This study (CORINE)
Habitats per area	Number of habitats per unit area	This study
Habitat dissimilarity	Dissimilarity of habitat proportions on focal island to the mean of historically inhabited islands	This study (CORINE)

Plant functional traits and indicator values

To evaluate the roles of plant functional traits in plant colonization ability, we compiled data from public plant trait databases (LEDA by Kleyer et al. 2008; Ecoflora by Fitter and Peat 1994) and existing literature (Ellenberg 1991, Hämet-Ahti et al. 1998). These compiled data included functional traits that influence plant competition, persistence and dispersal ability (Table 2). The traits related to competition and persistence included seed bank persistence, species' lifespan, life-form, specific leaf area (SLA), plant height and ability to reproduce vegetatively. Dispersal traits included seed mass, pollen vector, seed dispersal vector and ability to reproduce apomictically. For the numerical traits except for plant height, we calculated the mean of the validated measurements in the databases. For plant height, we used the maximum height according to Hämet-Ahti et al. (1998) to get the most accurate estimate in local growing conditions.

In addition to functional traits, the compiled data contained different indicator values of the species' ecological preferences (Table 2). We used Ellenberg indicator values for light, temperature, soil moisture, soil reaction (pH) and nitrogen (Ellenberg 1991). We also recorded the northern limit of each species' distribution in Finland from Lampinen and Lahti (2018) and its historical range size as the number

of islands that were occupied in the historical inventory. We further divided the species into functional groups based on their relationship to human cultural impacts and main growing environments (shore versus non-shore species). We transformed Eklund's (1958) codes for relationships to human cultural impact into an ordinal scale ranging from 1 to 7. Grouping to shore and non-shore species was based on field experience (MvN) and a classification developed by Palmgren (1961), and it has been used previously in von Numers (2011).

Based on plant traits and indicator values, we calculated the average trait dissimilarity between each potentially colonizing species and every resident species for each previously uninhabited island (Gowdis traits in Table 2). The mean dissimilarity was divided by the standard deviation of trait dissimilarities among the resident species to yield a metric that indicated how different the traits of the potential colonizer were compared to those of the resident species. Trait distance was based on Gower's (1971) metric, which Podani (1999) generalized to include factorial traits, and was calculated using the *gowdis*-function of the *FD* package (Laliberté et al. 2015) in R (R Core Team). All traits in Table 2, except for Historical total (i.e. the total number of islands inhabited by the species in the first inventory), were included in the calculation of Gowdis traits.

Table 2. Plant functional traits, Ellenberg indicator values, and other variables describing species' ecological preferences. Scale (N=numeric, C=categorical), description of each trait or classification/indicator value, and source of information are given. LEDA (Kleyer et al. 2008) and Ecoflora (Fitter and Peat 1994) are online databases, while all other sources are publications.

Name	Scale	Description, categories or unit	Source
Functional traits			
Life-form	C	Grass, herb, woody	Hämet-Ahti et al. 1998
Life-cycle	N	Long-lived or short-lived (incl. both annuals and biennials)	Hämet-Ahti et al. 1998
SLA	N	Specific leaf area: mm ² , mg ⁻¹	LEDA
Plant height max	N	Plant maximum height: cm	Hämet-Ahti et al. 1998
Vegetative reproduction	C	Does the species reproduce vegetatively: yes/no	Ecoflora and Hämet-Ahti et al. 1998
Apomictic	C	Does the species reproduce apomictically: yes/no	Hämet-Ahti et al. 1998
Seed mass	N	Seed mass, mg	LEDA
Seed bank	C	Persistent, transient, unknown	LEDA
Pollen vector	C	Insect, self, abiotic, abiotic and insect, abiotic and self, insect and self	Ecoflora
Dispersal vector	C	Seed dispersal vector: autochorous, endozoochorous, epizoochorous, myrmerochorous, wind and water, unspecialized	LEDA and Ecoflora
Indicator values			
Ellenberg's indices	N	Ellenberg's indices for plant species' environmental preferences (scale 1–9)	Ellenberg 1991
– light	N	Light	
– temperature	N	Temperature	
– moisture	N	Soil moisture	
– reaction	N	Soil reaction (pH)	
– nitrogen	N	Soil nitrogen	
Eklund culture	C	Human cultural impact: ordinal 1–7	Eklund 1958
Shore	C	Main growing environment is shore: yes/no	von Numers 2011
Other variables			
Historical total	N	Number of islands inhabited by the species in the first inventory	This study
North limit	N	Northern limit of species distribution in Finland: degrees latitude	Lampinen and Lahti 2018
Gowdis traits	N	A dissimilarity metric to compare species based on several traits (see text for details)	This study

Modelling colonization success relative to the colonization status of an island

We first explored the general pattern of colonization separately for species and islands by regressing a) the proportion of successful colonizations per island on the number of resident species in the first inventory, and b) the proportion of recently colonized islands on the number of islands the species occupied in the first inventory. Since the available data did not allow us to rule out a priori the colonization of any species from any island, we assumed that any species could potentially colonize all islands from which it was absent in the first inventory. We counted the number of successful colonizations out of all possible cases and transformed these counts to proportions of species and islands. We used proportions to avoid a spurious negative relationship between colonization success and the number of species or islands that would result from the potential exhaustion of the regional species pool (for the most species-rich islands) or uncolonized islands (for the most widely distributed species).

Modelling colonization success based on island properties and species traits

For each species-island combination, we recorded the colonization outcome and used it as a binomial response variable (success or failure) that we attempted to explain with island properties and species traits (Table 1, 2). We focused only on the main effects because the large number of missing values for species traits made an exhaustive search of even pairwise interactions unfeasible and caused convergence problems (see Supplementary material Appendix 1 Fig. A3 for the full model). Since habitat proportions summed up to 100%, they were inherently dependent on each other. We resolved the dependency by removing the scrub habitat from the explanatory variables, which allowed the remaining habitat proportions to vary relatively freely because scrub usually represented a large proportion of island area. We also ran the model fitting with scrub included, but this resulted in scrub being removed from the final model. We thus considered scrub to be relatively inconsequential to species' colonization, and do not believe that its removal from the initial model biased the analysis. We included species and island names as random factors to account for the multiple occurrences of each species and island in the colonization events. Moreover, we accounted for phylogenetic dependencies by nesting species within genus (nesting genus further within family was not considered due to zero variance). The associated intercept values allowed species to be ranked by any colonization ability that was not explained by traits, and the islands by any susceptibility to colonization that was not explained by their properties. Numeric variables were $\log_{10} x$ transformed if their distributions were strongly right-skewed, or $(\log_{10} x + 1)$ transformed if the original values included zeros. All numeric variables were then transformed to zero-mean and unit-variance to facilitate the comparison of their respective parameters in the fitted model.

The data on plant traits had missing values, particularly for rare species that occurred on only a few islands; such species represented potential new colonizers to a larger number of islands than did common species that already occupied most islands. Rare species were therefore overrepresented in the analyses of potential colonization compared to common species. Ellenberg's indices were missing from 56.8% to 73.4% of the potential colonizers, while other plant traits were sporadically missing from 53.9% of the cases in the full dataset of 587 plant species.

We had complete data for all island properties, with the exception of distance to the nearest historically colonized island; this value was missing from 10.2% of the colonization events where the species in question was not reported in the first inventory.

We used the Akaike information criterion (AIC) for model selection. The drop1-function of R software that we used for removing unimportant variables from the model did not allow missing values. Therefore, we omitted missing observations (i.e. potential colonization events) from the explanatory variables present in each model simplification step. To complement this analysis, we also report the full, unsimplified model (Supplementary material Appendix 1 Fig. A3). For the two analyses described above (AIC-simplified and full model), we fitted a generalized linear mixed model with binomial errors using the glmer function of the lme4 package (Bates et al. 2015) in R. We set the number of adaptive Gauss-Hermite quadrature points to zero ($nAGQ=0$) for computational efficiency during model simplification, and refitted the same model with the default $nAGQ=1$ (i.e. Laplace approximation) to ensure more accurate parameter estimates. Multicollinearity among explanatory variables was assessed as a variance inflation factor (VIF) calculated with the usdm package (Naimi et al. 2014). Various threshold values of VIF have been proposed (O'Brien 2007, Zuur et al. 2010) and we settled on excluding variables with $VIF > 5$. In the full model, most of the explanatory variables had $VIF < 3$, indicating that severe multicollinearity was unlikely.

We evaluated a species' colonization ability as a) the number of new islands colonized, b) the proportion of potential islands colonized and c) the magnitude of the species random effect in the colonization model, which measured variation in colonization probability that was explained by species identity after consideration of its traits. We made a similar assessment of islands' receptiveness to colonizers by counting a) the number of new species, b) the proportion of successful colonizations out of all potential colonizers and c) the magnitude of the island random effect, which measured the variation in the colonization probability among islands that was not explained by island properties.

Finally, we tested for spatial autocorrelation in the residuals of the simplified colonization model in order to see if colonization on adjacent islands is similar for reasons that could not be explained by other variables of the model. For this purpose, we calculated Moran's I (Moran 1948), weighting the index by inverse distance between islands. The existing R-functions known to us would generate

distance matrices that are computationally unfeasible with the current data ($n=85\,063$) and would not account for the repeated occurrence of the same islands in numerous colonization events. We therefore rewrote the ‘Moran.I’ – function of the ape-package (Paradis and Schliep 2018) with loops to avoid large matrix operations and with the number of islands ($n=471$) as the basis of the index SD and p-value in order to reduce the effect of island repetition.

Results

Modelling colonization success relative to the colonization status of an island

Islands were not saturated with species; there were, on average, 478 (range: 291–582) potential colonizing species per island out of the regional pool of 587 species (Fig. 2a). Generally, less than 20% of the potential colonizers were successful and 5–10% success rates were most common. The larger the number of resident species on an island, the higher the proportion of successful colonizers, despite the fact that species-rich islands had fewer potential colonizers in the species pool (Fig. 2a). The number of islands inhabited by a species was highly variable (Fig. 2b), resulting in a wide range in the number of new islands (11–471) colonized by different species, with an average of 384 newly colonized islands per species. A large number of species occurred on only a few or a few dozen islands, leaving numerous islands as potential new targets for colonization. The colonization of available islands increased strongly with the number of islands previously colonized (Fig. 2b).

Modelling colonization success based on island properties and species traits

The final statistical model (simplified by AIC) contained 13 fixed variables that explained plant colonization (Table 3). The sum of the absolute value of the explanatory variable coefficients, which quantifies the combined effect on colonization probability, was higher for the variables describing species’ historical distributions (1.778) than that for island properties (1.453) or species traits (1.046). New colonizations were thus better explained by colonization history and island properties than by species traits. Notably, the historical number of resident species per unit area was absent from the final model and did not sufficiently explain colonization success (Table 3, Fig. 3). Island variables that were positively related to colonization success included area of the recipient island, land area within a 2-km buffer of the recipient island, shoreline convolution, and the presence of limestone. Distance to the nearest previously colonized island was the single most important factor that was negatively associated with colonization success. The land cover classes decreasing colonization included sand and open or rocky habitat. Colonization decreased with increasing human cultural impact (Eklund culture) and to the east (EUREF X). Species’ historical distribution increased colonization success, as did plant height, vegetative reproduction, and a high Ellenberg value for nitrogen. The explanatory variables were often correlated (Supplementary material Appendix 1 Fig. A1, A2), but collinearity did not compromise the results as the maximum VIF-value was 1.68 (for distance to historical habitat). There was no significant spatial autocorrelation in the residuals of the simplified model based on Moran’s index ($I_{\text{obs}} = 0.00073$, $I_{\text{exp}} = -0.00213$, $SD = 0.00248$, $p = 0.2507$).

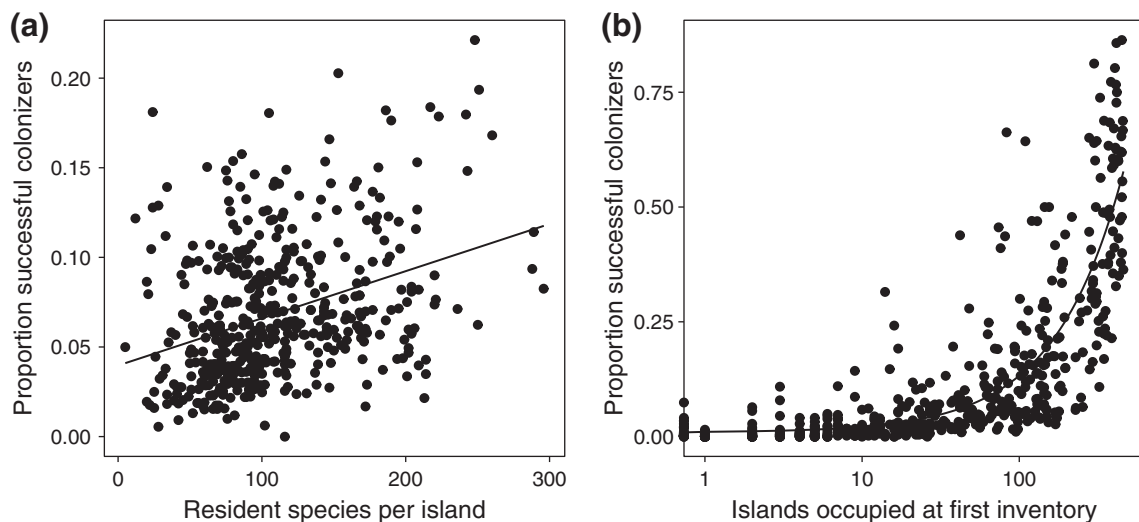


Figure 2 (a). The proportion of successful colonizers as a function of the number of species on an island in the first inventory. The fitted regression line $y = 2.63 \times 10^{-4} x + 3.97 \times 10^{-2}$ has the coefficient of determination $R^2 = 0.12$. (b) The proportion of successfully colonized islands as a function of the number of islands colonized at the time of the first inventory. The regression line $y = 1.24 \times 10^{-3} x + 9.10 \times 10^{-3}$, with $R^2 = 0.72$, was fitted to untransformed values of the x-axis, and drawn with a log-scale for clarity.

Table 3. Results from the generalized linear mixed model of the colonization success of 587 vascular plant species in the archipelago of SW Finland. Theoretical coefficient of determination, estimated with the MuMIn package, was $R^2=0.36$ for the model containing only fixed effects and $R^2=0.55$ for the model that included random effects. See Table 1 for descriptions of variables.

Coefficient	Estimate	Std. Error	z-value	Pr(> z)
Fixed effects				
(Intercept)	-3.510	0.122	-28.891	< 0.0001
Dist. to historical (log)	-0.751	0.022	-34.470	< 0.0001
Historical total (log)	1.026	0.070	14.694	< 0.0001
Area (log)	0.533	0.037	14.525	< 0.0001
Sand	-0.180	0.035	-5.118	< 0.0001
Open rock or bare ground	-0.204	0.039	-5.286	< 0.0001
Buffer 2 km (log)	0.166	0.037	4.544	< 0.0001
Plant height (log)	0.337	0.087	3.877	< 0.0001
Ellenberg nitrogen	0.247	0.074	3.346	0.0008
Convolution	0.107	0.033	3.263	0.0011
EUREF X	-0.085	0.031	-2.766	0.0057
Veg repr (yes)	0.312	0.143	2.188	0.0287
Limestone (yes)	0.178	0.076	2.336	0.0195
Eklund culture	-0.150	0.074	-2.029	0.0424
Random effects				
Groups	Variance	Std. Dev.	N	
Island	0.312	0.559	471	
Species:Genus	0.950	0.975	255	
Genus	0.132	0.363	153	
Total			85 063	

Inspection of the random effects in the final model revealed that variance among species was higher than variance among islands (Table 3), indicating that island properties were better able to explain differences in colonization success than species traits were. Not surprisingly, species differed greatly in their colonization ability, with 66 species not colonizing any new islands, while the top three species colonized around two hundred or more: *Odontites litoralis* (256 out of 388 potential islands, i.e. 66.2%), *Aster tripolium* (233/362 = 64.4%) and *Atriplex prostrata* (188/429 = 43.8%) (Supplementary material Appendix 2). The random effect size for species had a standard deviation of 0.87 (zero mean),

with the largest values found for *Centaureum littorale* (2.16), *Artemisia vulgaris* var. *vulgaris* (2.13) and *Rhinanthus serotinus* (2.12) (Supplementary material Appendix 2), suggesting that these species were more successful colonizers than could be explained by the available trait data. The smallest values of the random effect were found for *Juncus ranarius* (-1.91), *Carex pallescens* (-1.81) and *Alopecurus geniculatus* (-1.74), suggesting that these species underperformed as colonizers relative to their functional traits. Likewise, islands differed in their probability of becoming colonized (Supplementary material Appendix 3), and this probability seemed to be independent of distance to the mainland (Fig. 1b).

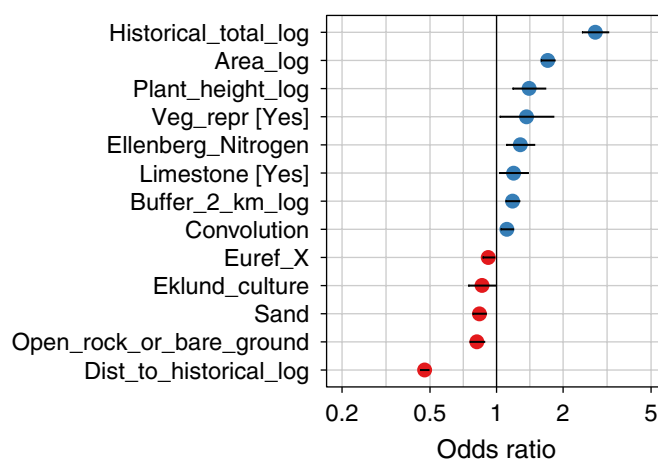


Figure 3. Odds ratios (i.e. $\exp[\text{parameter estimate}]$) and $\pm 95\%$ confidence intervals for the fixed effects of the colonization model. A positive value for which the confidence interval does not overlap zero indicates that the variable increases colonization probability. Variables are selected based on their change in AIC; observations with missing data were removed at each step. See Table 1, 2 for descriptions of variables and Methods for details of model selection.

Discussion

This long-term study spanning about 70 yr in the archipelago of SW Finland reveals that plant colonization success in this period depended most on species' historical distributions and island properties, with plant functional traits playing a smaller role. For example, colonization success correlated positively with island area and the historical number of islands colonized. The number of historically colonized islands and distance to the nearest historically colonized island were the most important explanatory variables associated with colonization success, indicating that seed dispersal might limit plant colonization in the Finnish archipelago. This observation was further supported by plant height, which correlates positively with seed dispersal distance (Thomson et al. 2011), being the trait with the strongest relation to colonization success in the present study.

Area and degree of isolation are fundamental components of the theory of island biogeography (MacArthur and Wilson 1967). As predicted, we observed that colonization success increased with increasing size of the target island, and decreased with increasing distance to the nearest previously inhabited island. Together these two variables were far more important in explaining colonization success than any measure of island quality or species habitat requirement. Similar to our finding, previous studies have reported that connectivity is critical for species colonization in patchy environments (Honnay et al. 2002, Aggemyr and Cousins 2012), suggesting that long-distance dispersal rarely leads to successful colonization. Moreover, high proportions of sand and open or rocky habitats reduced species colonization of an island, which is easy to understand since these habitats are harsher than the other habitats examined in the present study and lack organic soil, which makes them viable only for a few species. The importance of soil was also evident in an earlier study on a subset of the present islands, where insufficient depth of topsoil prevented tree vegetation (Hannus and von Numers 2008). The positive effect of limestone on colonization in the present study further supports this interpretation.

The decrease in colonization success to the east may reflect a more stable land use here compared to the west, where habitat changes associated with an almost complete ending of formerly intense cattle grazing may have resulted in a larger number of colonization. Our attempt to explain colonization with variables that measured the similarity between species' habitat requirements and the availability of habitats on potential new islands was not successful. This may partly be due to the coarseness of the habitat occupancy metric, as an island historically occupied by a species may include multiple habitats in which that species does not occur. This will bias the metric of habitat requirements and reduce its explanatory power. When a species requires a specific key habitat, its existence on the target island is likely to be more important than the island's general similarity to previously inhabited islands. Unfortunately, the spatial resolution of the data did not allow us to model habitat specificity at this level.

We found no relationship between the number of resident species per island area and colonization success. Thus, our results do not support the extrinsic determinants hypothesis, which predicts that environmental heterogeneity leads to a positive species diversity–colonization relationship (Naeem et al. 2000, Davies et al. 2005). In addition to species diversity, high trait similarity between colonizing and resident species might either enhance or reduce colonization success (Elton 1958, Proches et al. 2008). However, in the present study, trait similarity between potential colonizers and resident species did not explain colonization success. This is not particularly surprising because plants with both similar and different traits are generally able to coexist on the spatial scale of the study islands, and only a few traits on their own were able to explain colonization success.

The species traits that best explained colonization success on the islands included plant height. Height increases competitive ability for light and seed dispersal distance (Thomson et al. 2011), being a beneficial trait to both reaching new islands and succeeding in competition with the resident species. Moreover, increasing plant height is probably associated with a combination of grazing abandonment and natural succession resulting in a higher plant cover in the study area. Contrary to our predictions, other plant traits that reflect a species' colonizing ability, such as seed dispersal vector, seed number or seed size (Saatkamp et al. 2019), did not emerge as significant explanatory variables in the models. Previously, seed mass has been found to promote seedling establishment in multispecies experimental plant communities (Thompson et al. 2001, Kempel et al. 2013). However, the negligible effect of seed size on colonization success in the present study may not be that unexpected, given that its explanatory power is usually small compared to that of plant height (Thomson et al. 2011). In addition to plant height, vegetative reproduction increased colonization success in the present study, allowing a species to reproduce and persist in a new location in the absence of conspecifics. This trait reduces the strength of the Allee effect (Courchamp et al. 2008) in initially small colonizing populations and facilitates their establishment. The association of a high Ellenberg value for nitrogen with colonization success suggests that species requiring fertile soils are better colonizers than species adapted to lower nutrient levels. The same finding was made in a previous study, which compared plant species that had increased in frequency to those that had declined in frequency (von Numers and Korvenpää 2007). In that study, the shore species that became more abundant exhibited higher Ellenberg values for nitrogen than those that had declined. The lower colonization ability of species associated with cultural impact probably reflects the decline of grazing that was once prominent on the larger islands of the study area (von Numers and Korvenpää 2007).

Because we analyzed a large number of explanatory variables, for which a high proportion had missing values, the present study focused on the overall effects of island properties and plant functional traits on species colonization. However,

interactions between the two groups of variables (as well as within each group) are likely. As an example, Auffret et al. (2017) observed in the Swedish archipelago that the plant traits responsible for plant immigration to islands closer to the mainland were partially different from those responsible for immigration to remote islands. Trait interactions between invaders and the recipient community were also important in a seed sowing experiment in a savannah, where community traits were sometimes more important than invaders' traits in determining invasion outcome (Catford et al. 2019).

A species' colonization history was an important predictor in the present study: widely distributed species in the archipelago were most likely to colonize new islands. This observation mimics reports of invasive species, in which invasion history (i.e. whether the species is invasive in many countries) is among the most successful predictors of future invasibility (Hayes and Berry 2008). Together, island properties and a few species traits explained about 36% of overall colonization success (Table 3). However, when island and species identity were considered as random factors in the model, about 55% of the variation could be explained. Such an increase in explanatory power suggests that species identity may be a useful predictor of future colonization events, as the 587 vascular plant species considered here clearly differed in their colonization success. The importance of species-specific traits has been reported also for invasive plant species (Diez et al. 2008).

In conclusion, this study emphasizes that plant colonization on islands is more associated with island properties and species' historical distributions than with species' functional traits. While plant traits related to dispersal and establishment may enhance colonization, our results suggest that predictions of future changes in plant communities and analyses of plant colonization primarily require understanding of habitat properties and species' historical distributions.

Data availability statement

Data available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.fbbg79cr6>> (Aikio et al. 2020).

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Supplementary material (available online as Appendix ecog-05013 at <www.ecography.org/appendix/ecog-05013>). Appendix 1–3.