RESEARCH ARTICLE

Mixed evidence for the small-island effect in a replicated colonisation experiment

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Abstract

Aim: Plant species richness increases with island/patch area, but the effect of spatial scale on the shape of the species–area relationship remains debatable. We asked whether the small-island effect (SIE; i.e. different relationship between island area and species richness on smaller compared to larger plots) occurs in plants naturally colonising extremely small de novo plots.

Location: Northern Europe.

Methods: We established 16 experimental plots with bare ground (two plots of each of eight sizes, from 2 to 0.01 m^2) in each of four localities, and monitored colonisation of these plots by vascular plants from 2008 to 2010. We modelled species–area relationships in these plots by linear and breakpoint regressions, and we analysed plant functional traits with respect to plot size.

Results: Small-seeded plants were over-represented among the primary colonisers, and plant functional traits changed with plot size. On average, the number of plant species was six times greater in our largest (2 m^2) than in our smallest (0.01 m^2) plots. The SIE was observed in half of our analyses; the semi-log models identified SIE more often than the log-log models did (71.1% and 28.9% of all analyses respectively).

Conclusions: The evidence for the small-island effect in boreal forest plants colonising patches of bare ground is mixed. Despite extremely small patch size and habitat uniformity, half of our data showed a "classic" species–area relationship. Our findings hint that the probability of SIE occurrence increases with decreases in the species pool of primary colonisers and with decreases in the time from the beginning of colonisation. We suggest that the analysis of plant functional traits in study systems where SIE does occur be conducted to uncover the drivers of this interesting biogeographical phenomenon.

KEYWORDS
among-year variation, boreal forests, colonisation experiment, northern Europe, small-island effect, species richness, species–area relationship, vascular plants

1 | INTRODUCTION

Deciphering the mechanisms that shape richness and diversity of species assemblages is among the key goals of plant community ecology (Boeken & Shachak, 1998). These mechanisms are generally searched for by means of manipulative studies, including colonisation experiments (Boeken & Shachak, 1998; Joshi et al., 2006; Cichini et al., 2011) and experimental assembling of plant communities with different properties (Hector et al., 1999; Ben-Hur & Kadmon, 2020; Catano et al., 2021). At the same time, an experimental approach is rarely used in island biogeography (but see Simberloff, 1976; Loo et al., 2002; Hurlbert, 2006; Ben-Hur & Kadmon, 2020); rather, this research is primarily based on studying the outcomes of unintentional colonisation and extinction experiments (MacArthur & Wilson, 1967; Thornton, 2007; Whittaker et al., 2017).

Island (or patch) area is one of the key factors that affects the species richness of vascular plants, and the species–area relationship forms the core of island biogeography theory (MacArthur & Wilson, 1967; Warren et al., 2015). Without question, larger islands or patches, on average, accommodate more plant species than smaller islands or patches do (Sólymos & Lele, 2012), but the effect of spatial scale on the shape of the species–area relationship remains debatable (Whittaker et al., 2017). This is especially the case for "small" islets and habitat patches, where the species richness may vary independently of the island area (Lomolino, 2000; Lomolino & Weiser, 2001; Wang et al., 2018). This phenomenon, described by a linear breakpoint model with zero slope below the threshold (breakpoint) and a positive slope above it (Dengler, 2010), is called the small-island effect (SIE). However, some authors expand this definition and classify any difference in relationship between island area and species richness on smaller compared to larger islands, including situations when both slopes differ from zero (Matthews et al., 2020). Following Dengler (2010), we name these two definitions of SIE as SIE sensu stricto and SIE sensu lato, respectively.

The power-law species–area relationship is supported by hundreds, if not thousands, of studies (Drakare et al., 2006; Triantis et al., 2012; Matthews et al., 2019). Therefore, the exceptional behaviour of some study systems that show deviations from this pattern has multiple implications for both fundamental and applied ecology (Warren et al., 2015) and deserves a detailed exploration. So far, the occurrence of SIE has only been detected in natural ecosystems (including those modified by human impact), and the absence of experimental data further limits the identification of conditions under which SIE may occur. For example, the slope of the species–area relationship at small spatial scales decreases with a decrease in the pool of species available for colonisation (Catano et al., 2021); consequently, SIE may be expected to emerge when this species pool is extremely small.

The species–area relationships in plant communities can also depend on plant functional traits (Schrader et al., 2020). At smaller spatial scales, interspecific interactions (i.e. competition) are especially important (Grime, 1973), particularly when plants are fully sessile (van der Maarel & Sykes, 1993). With enlarging area, the role

of interspecific interactions typically weakens and environmental heterogeneity becomes the main determinant of species richness (Schmida & Wilson, 1985). Analysing plant traits relevant to competitive ability, resource uptake and dispersal at different spatial scales could potentially bring new insights into the relative role of biotic interactions and environmental filtering over the course of plant colonisation.

Colonisation is one of the key eco-evolutionary processes that shape the taxonomic and functional compositions of insular biota (MacArthur & Wilson, 1967; Whittaker et al., 2017; Ottaviani et al., 2020). In this study, we report the outcomes of a replicated colonisation experiment that was established to test three hypotheses regarding SIE. Based on the definition of SIE and on the properties of previous study systems that have reported SIE, we predicted that: (a) the species richness of vascular plants naturally colonising extremely small (0.01–2 m^2) plots created by the experimenter (de novo islands, as defined by Warren et al., 2015) does not depend on the plot area; (b) SIE is more likely to occur in species-poor than in species-rich source communities; and (c) SIE emerges in the early stages of colonisation of de novo islands but disappears later on, when plant–plant interactions take the leading role in shaping community composition. To uncover the mechanisms behind the detected species–area patterns, we asked whether the functional traits differ between plants that colonise our experimental plots and plants that form the surrounding (source) communities. We also questioned whether plot size affects these trait syndromes in a predictable manner.

2 | METHODS

2.1 | Study sites and experimental design

The four experimental sites were selected in northern Europe (Figure 1) at the northern (Kevo and Apatity) and southern (Seili and Lisino) borders of the boreal forest zone (Appendix S1). The experimental plots (16 per site; two plots of each of eight sizes) were established in June 2008 within the premises of ecological field stations to minimise the risk of vandalism. We created the larger plots (2, 1, 0.5 and 0.25 m^2) by excavating the ground to a depth of 15 cm, covering the excavation with polypropylene landscape fabric (90 g m^{-2}) and then placing commercially available soil over this fabric (Figure 2a,b). For smaller plots (0.1, 0.05, 0.02 and 0.01 m^2), we used plastic pots of appropriate size, inserted them into the soil and filled them with the same commercial soil (Figure 2c,d). Both these methods assured that plants colonising our plots emerged from airborne seeds and/or vegetative propagules rather than from the soil seed bank. The ground used in this experiment (Kevo and Seili: musta multa [BIOLAN Oy, Eura, Finland]; Apatity and Lisino: garden lux ground [Antey, Lomonosov, Russia]) did not contain live seeds, as confirmed by its exposure in a greenhouse.

The plots were surveyed five times: in late summer of 2008, 2009 and 2010 and in early summer of 2009 and 2010. During each survey, all plots were photographed and all plants in each plot were

identified and recorded. When a plant observed in early summer was too small to allow reliable identification, its position in a plot was recorded, and this plant was identified later in the summer. We also recorded all vascular plant species within a circle of 50-m diameter centred at experimental plots (termed the source community hereafter).

The following functional traits were extracted from the LEDA (Kleyer et al., 2008) and CloPla (Klimešová et al., 2017) trait bases for the 190 vascular plant species recorded in our experimental plots and in source communities: adult plant height (m), seed weight (mg), lateral spread (cm year^{-1}), leaf dry matter content per leaf water-saturated mass (mg g^{-1}, LDMC) and specific leaf area (mm^2 mg^{-1}, SLA). The complete set of the five trait values was obtained for 151 species (79%) (Appendix S2).

FIGURE 1 Location of study sites

2.2 | Statistical analysis

We explored the sources of variation in the numbers of plant species (non-transformed in the semi-log model and $\log_{10}(n+1)$-transformed in the log-log model) in individual plots by linear ANCOVA (SAS GLIMMIX procedure; SAS Institute, 2009), with the study site and survey date as fixed effects and the $\log_{10}$-transformed plot area as a covariate. We then studied the species–area relationship in each of 19 data sets that were collected from four sites during five censuses. One of the 20 data sets (collected on 5 Aug 2010 in Lisino) was incomplete because several experimental plots had been vandalised by that date; therefore, that data set was excluded from our analyses. Both semi-log and log-log-transformed data were fitted by linear regression, breakpoint (segmented) regression with zero slope in the first segment (left-horizontal model hereafter) and shallow-slope (segmented) regression (SAS REG and NLIN procedures, respectively; SAS Institute, 2009), yielding a total of 114 models. We did not analyse the untransformed data because they were previously found to demonstrate a substantially lower proportion of significant species–area relationships than was observed with the semi-log and log-log data (Matthews et al., 2014).

We compared the linear and left-horizontal models to test for the existence of SIE sensu stricto (as defined by Lomolino & Weiser, 2001), whereas the comparison between linear and shallow-slope models allowed to identify SIE sensu lato. Residual variations of the paired linear and breakpoint regression models were compared using the Akaike information criterion corrected for small sample size (AICc; graphpad.com/quickcalcs/AIC1.cfm; Burnham & Anderson, 2002), with one degree of freedom subtracted from the breakpoint regression model as penalisation for the additional parameter. When a shallow-slope breakpoint model identified no
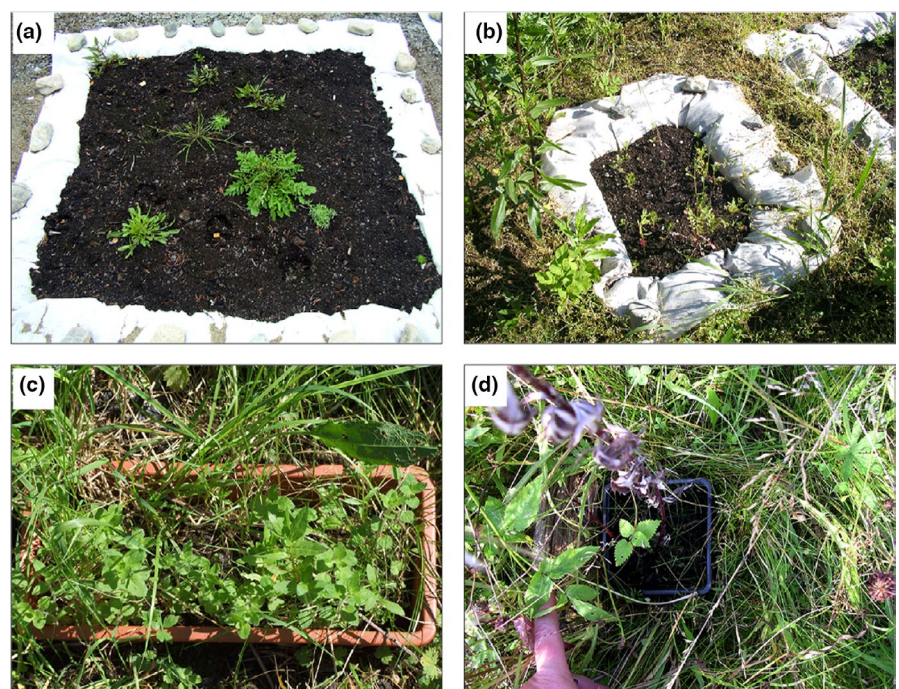

FIGURE 2 Examples of experimental plots: (a) Kevo, plot area 2 m^2, 2 Sep 2008; (b) Apatity, plot area 0.25 m^2, 16 Aug 2008; (c) Seili, plot area 0.05 m^2, 5 Jun 2010; (d) Lisino, plot area 0.01 m^2, 27 Aug 2009. Photos: V. Lanta (a, c) and V. Zverev (b, d)

threshold, the comparison was limited to linear and left-horizontal models. The species–area data set was classified as demonstrating SIE if the breakpoint regression model outperformed the linear model (Lomolino & Weiser, 2001; Triantis et al., 2012; Wang et al., 2018). We also compared the proportions of variation explained by semi-log vs. log-log linear models (SAS GLIMMIX procedure; SAS Institute, 2009) and calculated Pearson linear correlation coefficients between the numbers of plant species recorded in source communities and in our plots (SAS CORR procedure; SAS Institute, 2009).

The plant functional traits were averaged within a site for the source community, for all experimental plots combined and for experimental plots of each size. The log_{10}-transformed values of each trait were compared between the source communities and experimental plots by a paired t test and were then regressed for the log_{10}-transformed plot area. The choice between linear and quadratic regression models was based on AICc.

3 | RESULTS

In total, 96 species of vascular plants were recorded in 64 plots during the five surveys (Appendix S3). Overall, 18%–80% of these species were not found within 25 m of the centres of our experimental sites (Appendix S1), although all colonisers were common in the local floras of our study areas. The source communities jointly included 161 species (Appendix S3), and individual plots accommodated 0–23 species of vascular plants. The site-specific values of species richness in source communities and in experimental plots strongly correlated to each other ($r = 0.98$, $n = 4$ localities, $p = 0.014$).

The number of plant species varied with the locality, the date of the survey and the area of an experimental plot (Table 1). The number of plant species per plot in Kevo was about 20% of that in the other study sites (Figure 3a). Species richness peaked in the autumn of the second year and then decreased during the third study year (Figure 3b). Our smallest plots (0.01 m²) accommodated 2.13 ± 0.29 (mean ± SE) species, whereas our largest plots (2 m²) were populated by 13.15 ± 0.99 species.

The slope of the species–area relationship differed among study sites in both the semi-log and log-log linear models (site × area interaction in Table 1). The variation in slope among the five surveys was statistically significant for the semi-log models but not significant for the log-log models (survey × area interaction in Table 1). The average slope of the semi-log models increased from 3.33 in the first survey to 5.98 in the third survey, slightly decreased during the third survey (to 5.53) and then remained at this level during the fourth and fifth surveys (5.06 and 5.21 respectively; Appendix S1). The average slope of the log-log models was 0.306 (Appendix S1).

All 38 linear regression analyses (Appendix S1) revealed a statistically significant species–area relationship in our 19 data sets (Figure 4). Across these analyses, the explained variation did not differ between the semi-log and log-log models ($F_{1,36} = 0.17$, $p = 0.68$). The left-zero breakpoint regression model outperformed the linear model in 13 of 19 paired analyses of the semi-log data but only in six of the 19 paired analyses of the log-log data (Appendix S1, Figure 4), thus yielding a 1:1 ratio when two data transformations were combined. Across these 19 analyses, which yielded statistical evidence for the SIE sensu stricto effect, the threshold area (the area below which the species number was approximated by the zero-slope segment of the breakpoint model) was, on average, 0.179 m² (Appendix S1).

The shallow-slope breakpoint regression model outperformed the linear model in 14 of 19 paired analyses of the semi-log data but only in five of the 19 paired analyses of the log-log data (Appendix S1, Figure 4), thus yielding a 1:1 ratio when two data transformations were combined. Across these 19 analyses, which yielded statistical evidence for the SIE sensu lato effect, the threshold area was, on average, 0.223 m² (Appendix S1).

The left slope of the shallow-slope models was statistically significant in 12 of 31 data sets, indicating that the species richness of vascular plants often increased with the increase in plot area in those subsets of our data that were classified as demonstrating the SIE sensu lato effect. The variation explained by the best-fit model did not differ significantly ($F_{2,27} = 1.31$, $p = 0.29$) between linear ($R^2 = 0.84$), left-horizontal ($R^2 = 0.82$) and shallow-slope ($R^2 = 0.86$) models.

The seeds were smaller in the plants recorded in the experimental plots than in the plants from the source communities (0.42 and 0.78 mg, respectively; paired $t_3 = 6.68$, $p = 0.0022$). Within the experimental plots, the adult plant height and horizontal spread

Sources of variation	Degrees of freedom	Semi-log model		Log-log model	
		F	p	F	p
Site	3	199.0	<0.0001	141.9	<0.0001
Survey	4	26.8	<0.0001	8.49	<0.0001
Area (log_{10}-transformed)	1	834.7	<0.0001	773.2	<0.0001
Site × Area	3	40.9	<0.0001	7.60	<0.0001
Survey × Area	4	5.66	0.0002	0.29	0.88
Site × Survey	12	7.77	<0.0001	2.38	0.0062
Site × Survey × Area	12	1.93	0.0314	0.83	0.62
Error	274				

TABLE 1 Sources of variation in species richness of vascular plants (SAS GLIMMIX procedure, type 3 tests)
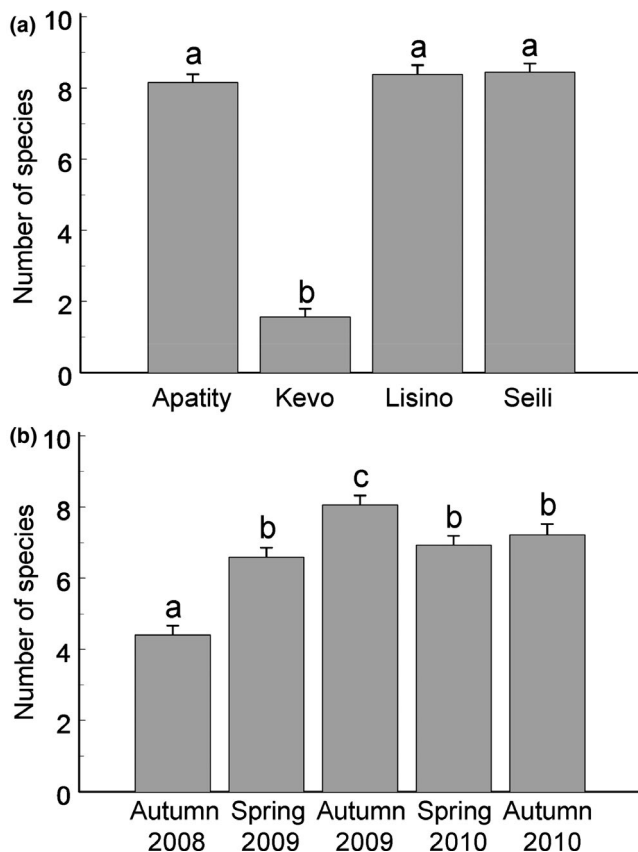
FIGURE 3 Numbers of vascular plant species averaged by (a) study sites ($n = 5$ censuses) and (b) by individual censuses ($n = 4$ sites). Bars indicate standard errors. Values labelled by different letters significantly ($p < 0.05$) differ from each other

increased with plot size, whereas SLA demonstrated a U-shaped pattern (Figure 5). No variation was observed in any plant trait in our study plots across the three study years ($p > 0.20$).

4 | DISCUSSION

The overall uniform increase in species richness with an increase in study area is so ubiquitous that, for a long time, this pattern was seen as one of the fundamental ecological laws (Lawton, 1999; Gotelli, 2001). However, Lomolino and Weiser (2001) suggested that this pattern is not uniform but is instead scale-dependent and that the species–area relationship differs fundamentally among three realms: (a) small islands where species richness varies independent of area (i.e. that demonstrate SIE sensu stricto); (b) islands beyond the upper limit of SIE, where richness varies in a more deterministic and pre-dictable manner with island area and associated ecological factors; and (c) islands that are large enough to provide the internal geo-graphical isolation necessary for in situ speciation.

During the past two decades, hunting for SIE has become increasingly popular, and — despite the publication of discon-firming (e.g. Jüriado et al., 2006; Panitsa et al., 2006) and incon-clusive (e.g. Barrett et al., 2003; Hannus & von Numers, 2008)

evidence — many researchers have concluded that SIE is a common ecological phenomenon both in true islands and in habitat patches (Wang et al., 2018; Gao et al., 2019). Nevertheless, even the pro-ponents of SIE agree that some data sets collected from small is-lets or patches are better fitted by a power-law model than by a segmented model (Lomolino & Weiser, 2001; Wang et al., 2018; Gao et al., 2019). They also concur that a segmented model, even when it outperforms the non-segmented models, often adds lit-tle to the explained variation (Barrett et al., 2003; Dengler, 2010), and our results support the latter conclusion. Thus, the prevalence and ecological importance of SIE require further investigation, because an adequate modelling of the species–area relationship is crucial not only for understanding global biodiversity patterns but also for developing a strategy of biodiversity conservation in a rapidly changing world.

The SIE is usually sought by fitting the species–area data with a piecewise regression model using two (Lomolino & Weiser, 2001) or even three (Gao et al., 2019) segments and comparing the per-formance of this segmented model with the performance of a non-segmented (usually semi-log or log-log) model. However, the performance of the breakpoint model above the so-called thresh-old area (which reflects the upper limit of SIE) is of little interest for the identification of the SIE. Nevertheless, only a few studies (e.g., Triantis et al., 2006) have separately explored the properties of this model below the identified threshold, where a substantial increase in island or patch area is presumably not accompanied by any signif-icant increase in species richness.

To our knowledge, the lowest threshold area of 50 m^2 was iden-tified for vascular plants on Hjälmaren Lake in Sweden (Lomolino & Weiser, 2001). Subsequent reviews reported that the lowest thresh-old areas in different data sets for different taxa were 1 348 m^2 (Wang et al., 2018; and personal communication), 1 450 m^2 (Triantis et al., 2006), 3 000 m^2 (Matthews et al., 2014) and 10 000 m^2 (Schrader et al., 2020). Therefore, we assumed that, in terms of SIE, our experimental plots that do not exceed 2 m^2 should *all* be clas-sified as "small". Therefore, a six-fold difference in the number of vascular plant species between our smallest (0.01 m^2) and largest (2 m^2) plots indicates the absence of SIE sensu stricto in our study system. Alternatively, we have to accept that our largest plots were still larger than the threshold area for our study system and that we must search for SIE in a subset of the smallest plots.

This search, based on the use of two breakpoint regression mod-els, identified SIE in half of the conducted analyses. However, the proportion of the data sets demonstrating SIE greatly depends on whether the number of species in our plots was log_{10}-transformed prior to the analysis. An equal percentage of variation in our data was explained by semi-log and log-log models, therefore we have no reason to prioritise our conclusions based on one of these two mod-els, despite the log-log models providing the best fit for the species–area relationships across hundreds of data sets (Triantis et al., 2012; Matthews et al., 2016). Across our data, log-log models identified SIE in 11 of 38 analyses (i.e. 28.9%), whereas the semi-log models identi-fied SIE in 27 of 38 analyses (i.e. 71.1%). Thus, we conclude that the
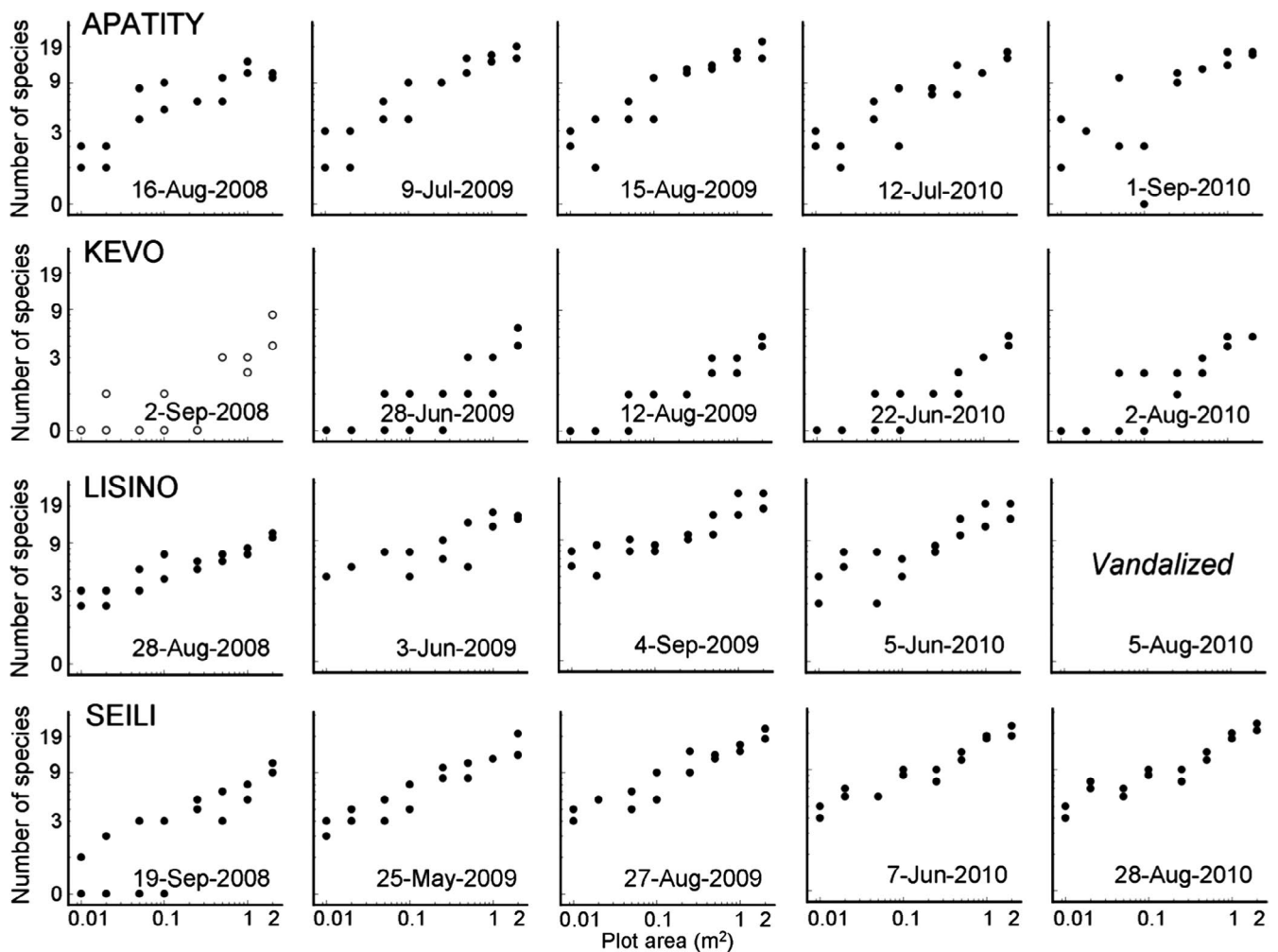
FIGURE 4 Numbers of vascular plant species in plots of different size during individual censuses across four study areas. For the characteristics of regression models consult Appendix S1

evidence for the small-island effect in our colonisation experiment is mixed, and that the prevalence of SIE (both sensu lato and sensu stricto) differs greatly between semi-log and log-log models. The latter result is in line with the previously published conclusion that the method of data transformation can greatly change the outcomes of studies exploring species–area relationship (Matthews et al., 2014). From a methodological perspective, we suggest that future studies should employ more rigorous statistical protocols (e.g., Triantis et al., 2006) to identify SIE in individual data sets.

Our second hypothesis regarding the prevalence of SIE in species-poor communities was based on the assumption that SIE might emerge when the number of species in experimental plots is limited by a small pool of colonisers. The strong positive correlation between the numbers of species recorded in source communities and experimental plots confirmed this conclusion, which is in line with weak relationship between the total number of shrub species and the island area in Nui Atoll explained by a limited pool of potential colonisers (Woodroffe, 1986). Recently, effects of the species pool were found on the species–area relationship in natural (Matthews et al., 2019) and experimental (Catano et al., 2021) systems. Not surprisingly, small species pools decrease the slope of the species–area relationship (Catano et al., 2021) to a value approaching zero, thereby making the occurrence of SIE more likely than in species-rich environments. In agreement with these studies, the prevalence of SIE was greatest in Kevo (66.7%), where the source community of vascular plants species included about one-third of that in other study sites (Appendix S3). The lack of replication does not allow us to unequivocally accept the second hypothesis; nevertheless, the collected data do not contradict it.

Ottaviani et al. (2020) recently suggested that a trait-based comparative approach has the potential to considerably further our understanding of plant ecology in insular systems. The analysis of functional traits revealed that species that produce small seeds were over-represented in our experimental plots relative to the source communities. Furthermore, the functional composition of the plant communities formed in our experimental plots changed in a predictable manner with plot size. These findings indicate that our hypothesis regarding the prevalence of SIE in species-poor communities was oversimplified because the number of species found in an island or habitat patch of a given size — even in the absence of isolation that
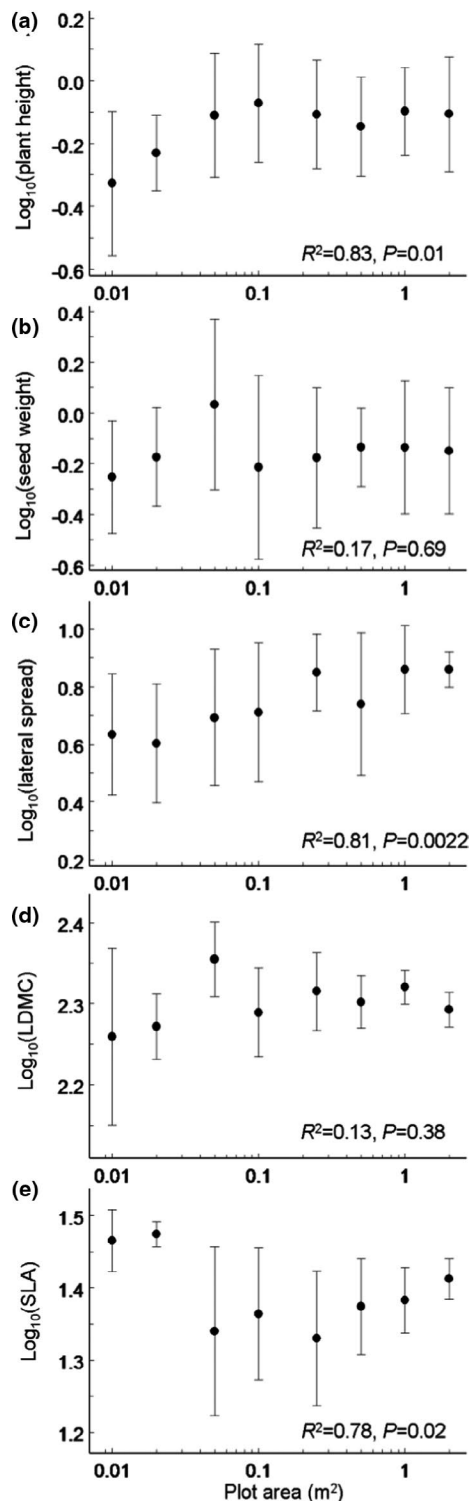
FIGURE 5 Plant functional traits (mean $\pm$ SE, $n = 4$ sites) in experimental plots of different size: (a) adult plant height (m), (b) seed weight (mg), (c) lateral spread (cm year^{-1}), (d) leaf dry matter content per leaf water-saturated mass (mg g^{-1}, LDMC), (e) specific leaf area (mm^2 mg^{-1}, SLA). The R^2 and p values refer to linear (b, c, e) and quadratic (a, d) models

shapes distinct functional composition in true island systems (Burns, 2019) — may depend on the number of species with particular functional traits rather than on the overall species richness.

During the first three censuses, fast-growing annuals and biennials (*Poa annua*, *Artemisia vulgaris*, *Epilobium angustifolium*) with higher SLA and greater plant height (traits related to above-ground competition for light) and lower LDMC (reflecting acquisitive strategies in resource use) were promoted in the majority of plots. These were accompanied, or gradually replaced, by perennial grasses (*Poa pratensis*, *Festuca rubra*) and woody plants (*Rubus idaeus*, *Salix rosmarinifolia*). This process may indicate an increasing importance of niche-based processes and a diminishing role of local species pool (at small spatial scales), plant dispersal abilities (affecting the probability of reaching study plots) and competition for light gradually increasing across seasons.

Our third hypothesis regarding the occurrence of SIE at certain stages of colonisation was based on among-species variations in the probability of arriving at the vacant habitat patches we had created. This probability could be affected by multiple factors, including species abundance near our plots, dispersal syndrome, seed mass and many other traits of potential colonisers (Eriksson, 2000; Butterfield et al., 2019). Observations on Mount St Helens demonstrated a rapid increase in species richness after the 1980 eruption, and the primary colonists in this region were dominated by long-lived perennials characterised by having light, wind-dispersed seeds (Miles & Walton, 1993). A similar pattern, in terms of seed weight, was also observed in our plots. Thus, the species pool of primary colonisers is likely limited, resulting in a higher probability of the occurrence of SIE at the early successional stages. This mechanism of SIE generation was also recently observed in trees colonising highly isolated courtyards in downtown St Petersburg, Russia (Kozlov & Zverev, 2022). However, our study provided only partial support for the third hypothesis, because the slope of the species–area relationships increased between the first and the second surveys only in the semi-log-transformed data.

The increase in species richness with an increase in the patch area is commonly attributed to three mechanisms: an increase in the number of individuals, an increase in the range of ecological conditions and a reduction in the extinction rates (Ben-Hur & Kadmon, 2020; and references therein). Our plots were homogeneous at the beginning of the experiment; therefore, we can exclude the second (habitat diversity) mechanism. Nevertheless, the size of our plots still affected both the number of species and their functional composition, as evident from the systematic changes noted in several plant functional traits with plot size (Figure 4). The third (extinction-based) mechanism is hardly applicable to our experiment, because none of our plots was large enough to support a distinct population of any vascular plant species. Therefore, we suggest that the "classic" species–area relationship in our experiment, as in the experiment by Ben-Hur and Kadmon (2020), emerged primarily due to the first mechanism and reflected a passive sampling effect.

To conclude, both SIE sensu stricto and SIE sensu lato were observed in a half of the analyses of species richness of boreal forest plants colonising experimentally created small patches of bare ground. Our findings hint that the probability of SIE occurrence increases

with decreases in the species pool of primary colonisers and with decreases in the time from the beginning of colonisation. We suggest that more rigorous approaches be used to detect SIE in both primary studies and research syntheses and that the analysis of plant functional traits in study systems where SIE does occur be conducted to uncover the drivers of this interesting biogeographical phenomenon.

AUTHOR CONTRIBUTIONS

MVK conceived the ideas, planned the study and coordinated data collection; MVK and VZ established the experiment; MVK, VL and VZ collected the data; MVK and VL performed the statistical analysis; MVK wrote the manuscript and all authors contributed to revisions. All authors have given their consent for the publication of this manuscript.

DATA AVAILABILITY STATEMENT

The data files are added in Appendices S2 and S3 (S2: Kozlov-etal-AppendixS2-071021.xls; S3: Kozlov-etal-AppendixS3-071021.xls).

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

Appendix S1. Plot characteristics and parameters of regression models

Appendix S2. Plant functional traits

Appendix S3. Occurrence of plant species in experimental plots