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Is the small island effect observed in the courtyards of a historical city centre?

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ABSTRACT
Growing evidence suggests that biodiversity on small islands and fragments could be independent of island area, a pattern called the Small Island Effect (SIE). We searched for SIE among the floras of 19 courtyards completely enclosed by buildings in central St Petersburg, Russia, in 1993, 2003 and 2008. Despite the extremely small size of the studied habitats (125–3500 m^2; open ground area 0.1–700 m^2), the number of native and naturalized vascular plant species generally increased with an increase in habitat area. Plant species richness was better explained by the open ground area than by the total courtyard area, and species–area relationships did not differ between ornamental and non-ornamental plants. The statistical support for SIE was obtained in 3 of 14 analyses. Both semi-log and log-log data demonstrated SIE in trees, but not in shrubs or herbs. We also found SIE in the 2008 data (all life forms combined), but only with a semi-log model. The threshold area for the detected SIE was 3–7 m^2. We conclude that SIE in urban green spaces may be an exception rather than the general rule. Its occurrence may be transient and may depend on the current balance of stochastic colonisation and extinction processes. Thus, even a minor increase in the area of open ground patches embedded in an urban matrix will increase the diversity of plants persisting in these patches. This finding justifies the importance of small local actions for maximizing the conservation of urban biodiversity and the retention of the ecosystem services it provides.

Introduction

Urbanisation has overwhelming impacts on ecosystems through habitat loss, deterioration of habitat quality (e.g. due to fragmentation and pollution) and changes in climate (Grimm et al. 2008; McDonald et al. 2013), making the recent conflict between urbanisation and biodiversity conservation priorities quite obvious. Although a high proportion of urban flora is selected and planted by humans (Novak 2012), a substantial part of ornamental species have naturalized in urban habitats (Byalt et al. 2019). Many species spontaneously established even in city beautification parks, which were created and constantly managed by landscape designers (Chang et al. 2021). The growing evidence shows that some species, including threatened ones, not only persist in urban habitats but flourish there (Schwartz et al. 2013; Ives et al. 2016). Plants in urban areas have high societal value (Hartig and Kahn 2016), and their conservation value grows with the expansion of urban areas (Goddard et al. 2010). Little is known, however, about characteristics of green urban areas that affect the ability of diverse species to persist in or colonise these areas (but see e.g. Williams et al. 2009; Planchuelo et al. 2020; Chang et al. 2021).

Habitat loss was recently identified as one of the five main drivers of biodiversity decline across the planet (IPBES 2019). However, despite a solid theoretical basis

accommodating both evolutionary and ecological phenomena (MacArthur and Wilson 1967; Whittaker and Fernández-Palacios 2007; Whittaker et al. 2017), the impacts of fragmentation (i.e. of a decrease in size of habitat patches and an increase in their isolation) on biodiversity recently caused a heated debate (Fletcher et al. 2018; Fahrig et al. 2019). This debate, in particular, stressed the need for further development of island biogeography, including testing the applicability of models developed for natural ecosystems to novel ecosystems (for definition, consult Teixeira and Fernandes 2020) formed in urban habitats.

The core of island biogeography theory is the species-area relationship (MacArthur and Wilson 1967). Many hundreds, if not thousands, of studies have demonstrated the generality of the power-law species-area relationship using either semi-log (species-log area) or log-log (log species-log area) data (Drakare et al. 2006; Triantis et al. 2012; Matthews et al. 2019). Nevertheless, numerous attempts have been made to refine the mathematical fit of the models describing this relationship (Lomolino 2000; Lomolino and Weiser 2001; McGill 2003; Chisholm et al. 2016; Gao et al. 2019; and references therein). In particular, one suggestion has been that the power law adequately describes species accumulation only in medium-sized to large islands and fragments, whereas

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the species richness on small islands may vary independently of island area (Lomolino 2000; Lomolino and Weiser 2001). This phenomenon is called the Small Island Effect (SIE hereafter).

The SIE hypothesis, which dates back to the 1960s and has been extensively discussed in the past (Woodroffe 1986), has gained greater acceptance following the work of Lomolino and Weiser (2001). These authors concluded that SIE is a relatively common phenomenon that occurs in 73 to 89% of the 102 studied data sets, depending on the transformation of the data used to identify SIE. However, subsequent studies pointed out several statistical and other methodological issues that may also explain this result (Burns et al. 2009; Dengler 2010; Tjørve and Tjørve 2011; Wang et al. 2016), suggesting that SIE is not as frequent as it had been found by Lomolino and Weiser (2001). In particular, the current review concluded that SIE occurs in 40% of the 90 studies of habitat islands (Wang et al. 2018).

The two-fold decrease in the proportion of studies demonstrating SIE over about two decades, from the seminal work by Lomolino and Weiser (2001) to the review by Wang et al. (2018), is in line with the general decline in effect size with the year of publication (Jennions and Møller 2002). The strength of the evidence supporting any theory fades with time, in particular because the "negative" and non-significant results may take longer to publish and are more difficult to locate due to the smaller visibility of the journals in which they are finally published (Jennions et al. 2013; Marks-Anglin et al. 2021). As a result, special efforts are required to make the publication portfolio representative of the actual findings. We therefore decided to open our file drives that contained multiple datasets collected long ago but never published due to either a complete absence of the expected SIE or a rare occurrence of it in our data. These results look trivial from the perspective of the classical theory of the power-law species–area relationship (MacArthur and Wilson 1967), but their publication will contribute to achieving a more balanced view regarding the SIE problem.

Urban habitats have been frequently compared to islands, because they are isolated from each other and from the surrounding natural habitats by built environment (Davis and Glick 1978). Consequently, the models of island biogeography have been repeatedly invoked to explain variations in species richness in different kinds of urban green spaces, primarily parks or forest fragments, by their size, isolation, and other properties (Pyšek 1998; Miyashita et al. 1998; Fernández-Juricic and Jokimäki 2001; Cook et al. 2002; Lizée et al. 2012; Medeiros-Sousa et al. 2017; and references therein). Importantly, direct human influence does not distort the species–area relationships: even in heavily managed city parks of Taipei, where landscape design was the major driver of plant diversity, park area appeared the most important factor explaining species composition and richness (Chang et al. 2021).

A recent review identified only two studies of plants in urban fragments that appeared suitable for searching for SIE (Wang et al. 2018), despite the importance of SIE for planning of conservation measures in highly fragmented urban landscapes. Keeping in mind the acute shortage of data on biodiversity of the smallest islets and fragments (but see e.g. Helden and Leather 2004), we designed the present study to test whether the species richness of vascular plants in small (125–3500 m^2), highly isolated courtyards in central St Petersburg, Russia is independent of the patch area, as predicted by SIE (Lomolino and Weiser 2001). We also asked whether plant species richness was better explained by the open ground area than by the total courtyard area, and whether the species–area relationships within the same set of courtyards varied between ornamental and non-ornamental plants, among study years and among plant life forms.

Materials and methods

Study area

St Petersburg (named Leningrad from 1924 to 1991), established in 1703 A.D. on previously unpopulated territory, had a population of about 5 million during the study period. No fragments of natural vegetation on primary soils persisted within a radius of 5 km from the city centre (Goryshina 2003).

The studied courtyards (Table 1) are situated in the downtown region, in an area that has been densely built for at least 150 years. Bolshaya Pushkarskaya Street is located close to two large parks (the Botanical Garden and Alexandrovskij Park), while Gorokhovaya Street is more than 2 km away from any parks. In both streets, we selected the most isolated (i.e. most resembling the islands) courtyards that were surrounded by buildings at least 10 m high and were connected to streets and other courtyards only by narrow arches. Care was taken to select courtyards of different areas and shapes and with different proportions of open ground.

Data collection

Data were collected in August–October of 1993, 2003 and 2008. In the 2010s, all these courtyards have been equipped with locked gates, which made further data collection impossible. The courtyard areas were measured in 1993, whereas the areas of open (i.e. unpaved) ground, including grass plots and flowerbeds, were measured during each survey

Table 1. Characteristics of investigated courtyards. Prior analyses, we added 0.1 m² to the measured area of open ground in each courtyard to account for non-measurable cracks in the pavement, which in some courtyards were the only habitats suitable for plants.

| | | | | Numbers of recorded species | | | | | | | | |
| | Area, m² | Open ground area, m² | | | Trees | | | Shrubs | | | Herbs | | |
Address	1993	1993	2003	2008	1993	2003	2008	1993	2003	2008	1993	2003	2008
Gorokhovaya 5	345	0	2	5	0	1	1	1	0	1	6	8	6
Gorokhovaya 12	255	200	3	85	2	1	3	3	0	3	8	2	12
Gorokhovaya 23	460	48	65	100	1	3	1	1	2	1	11	14	8
Gorokhovaya 25	155	0	5	0	1	2	0	0	1	0	6	15	7
Gorokhovaya 28	445	17	6	34	3	3	3	6	1	2	10	16	15
Gorokhovaya 30	350	3	0	6	0	1	0	2	0	1	4	6	9
Gorokhovaya 21	1260	180	182	175	6	5	4	1	0	6	2	11	23
Gorokhovaya 35	1680	200	700	503	6	6	5	7	4	1	19	11	33
Gorokhovaya 41	3500	270	510	311	5	5	7	1	0	1	11	3	17
Gorokhovaya 50	1885	288	245	487	2	7	7	5	8	7	18	24	32
Gorokhovaya 51	935	96	280	213	6	6	5	3	3	4	6	12	22
Gorokhovaya 69	200	25	36	55	2	3	3	2	1	2	8	8	18
Gorokhovaya 71	125	0	0	0	0	2	0	0	1	0	3	5	2
B. Pushkarskaya 31	545	3	0	0	1	1	0	1	0	0	6	2	1
B. Pushkarskaya 33	600	0	0	1	0	1	1	0	1	1	0	12	5
B. Pushkarskaya 40	870	186	195	235	3	5	3	5	4	2	11	18	26
B. Pushkarskaya 43	800	42	52	110	4	6	6	4	6	5	11	14	25
B. Pushkarskaya 45	235	0	0	0	0	2	0	0	0	0	1	4	0
B. Pushkarskaya 60	155	20	18	0	3	2	0	1	1	1	14	9	2

with a MeterMaster Laser (UMAREX[7] GmbH & Co KG, Arnsberg, Germany; accuracy <0.5%). We added 0.1 m² to the measured area of open ground in each courtyard to account for non-measurable cracks in the pavement as these, in some courtyards, were the only habitats suitable for plants.

Plants were recorded by one or two persons: M.V.K. and V. Neshataeva in 1993; V.Z. in 2003; and A. Stekolshchikov in 2008. Our colleagues involved in data collection (V. Neshataeva and A. Stekolshchikov) were not informed of the hypothesis being tested; instead, we told them that we were compiling a floristic list for the downtown area of St Petersburg. Trivial plants were identified *in situ*; the problematic specimens were collected or photographed and then identified using different guidebooks and pictorial keys. For mature trees, we measured the diameter at breast height; these data allowed us to follow the fate of individual trees from 1993–2008. Plant names (Data S1) follow Plants of the World Online (http://www.plantsoftheworldonline.org/).

We classified all species as either ornamental (i.e. not belonging to the native flora but often planted in gardens for the display of aesthetic features) or non-ornamental (i.e. those species whose occurrence in courtyards is primarily, but not exclusively, driven by natural colonization). The ornamental plants were further classified (according to Byalt et al. 2019) as naturalized (i.e. spontaneously colonizing new urban habitats) or not naturalized, whose occurrence is fully controlled by planting. We also classified the plants into three life forms: trees, shrubs and herbs (including grasses) (Data S1).

Data analysis

All our analyses of species–area relationships were based on the numbers of native and naturalized species, which can colonize new urban habitats without being planted by humans. We used ANOVA (SAS Institute 2009) to compare the areas of open ground and the numbers of plant species recorded in individual courtyards among three study years, as well as to compare the proportions of variation in species richness, which were explained by different classes of models. The linear Pearson correlation coefficients between species number and the total courtyard area or the area of open ground (averaged across three study years) were compared as described by Diedenhofen and Musch (2015). Based on the results of this comparison, we used the area of open ground as the explanatory variable in all subsequent analyses.

We checked whether the numbers of ornamental and non-ornamental plant species in individual courtyards correlated with each other during each of three study years. We also compared the slopes of the species–area relationships between these groups of plants by linear mixed model ANCOVA (SAS GLIMMIX procedure; SAS Institute 2009), with plant group as a fixed effect and the log-transformed area of the open ground as a covariate. The study site (i.e. the individual courtyard) was treated as a random intercept effect. We facilitated accurate F tests by adjusting the standard errors and denominator degrees of freedom by the latest version of the method described by Kenward and Roger (2009).

We compared the performance of linear regression and breakpoint (segmented) regression with zero slope in the first segment in seven data sets: 1) the average number of species of all vascular plants and the average area of open ground; 2)‒4) ibid., but separately for trees, shrubs and herbs (including grasses); and 5)‒7) the number of species of all vascular plants (+1 to allow analysis of zero species numbers) and the area of open ground separately for each study year. Both semi-log and log-log transformed data sets were fitted by linear regression and breakpoint regression models (SAS REG and NLIN procedures, respectively; SAS Institute 2009), yielding a total of 28 models. We did not analyse the untransformed data because they were previously found to demonstrate substantially lower proportion of significant species‒area relationships than semi-log and log-log data (Matthews et al. 2014).

Residual variations for 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 and Anderson 2002), with one degree of freedom subtracted from the breakpoint regression model as penalisation for the additional parameter. We also compared the proportions of variation explained by semi-log vs log-log models and by linear vs breakpoint regressions (SAS GLIMMIX procedure; SAS Institute 2009).

Absolute (TA) and relative (TR) turnover rates were calculated following Panitsa et al. (2008): $TA = (I + E)/2t$ and $TR = [(I + E)/t(S1 + S2)] \times 100$, where t is the period between censuses (i.e. 10 years between 1993 and 2003 and 5 years between 2003 and 2008), E is the number of species observed only in the first of the compared years (i.e. extinct between the first and the second observation), I is the number of species observed only in the second year, and S1 and S2 are the total numbers of species recorded in the first and the second year, respectively. The values of TA and TR were averaged between two study periods (1993‒2003 and 2003‒2008) and regressed against the average area of the open ground (SAS REG procedure; SAS Institute 2009).

Results

A total of 169 species of vascular plants (15 trees, 26 shrubs and 128 herbs and grasses) were recorded in 19 courtyards: 80 species in 1993, 89 species in 2003 and 126 species in 2008 (Data S1). Of these 169 species, 146 were native or naturalized; their numbers in individual courtyards were 0–27 in 1993, 3–35 in 2003 and 0–44 in 2008 (Table 1).

The number of courtyards with well-managed flowerbeds changed from two in 1993 to one in 2003 and to three in 2008. Only two trees were planted in all 19 courtyards between 1993 and 2008, whereas 30 trees were cut down (Table S1). The area of open ground ($F_{2, 54} = 0.38$, $P = 0.69$) and the number of plant species ($F_{2, 54} = 1.24$, $P = 0.30$) were similar across our courtyards in 1993, 2003 and 2008.

Ornamental plants (61 species) were generally less abundant than non-ornamental plants (108 species): each species attributed to these groups was recorded, on average, in 11% and 18% of courtyards, respectively. Two-thirds of ornamental plants found in courtyards (38 species) have naturalized in St Petersburg. The species richness of the ornamental plants was strongly and positively correlated with the species richness of the non-ornamental plants in each of the three censuses (1993: $r = 0.82$; 2003: $r = 0.83$; 2008: $r = 0.76$; for all correlations, $n = 19$ courtyards and $P < 0.0001$), and the slope of the species–area relationships did not differ between these two groups of plants ($F_{1, 92.5} = 0.01$, $P = 0.92$).

Both semi-log and log-log regression models demonstrated that the variation in plant species richness (native and naturalized plants combined) is better explained by the open ground area than by the total courtyard area (Figure 1). The differences in the Pearson correlation coefficient between the species number and these two explanatory variables (the open ground area and the total courtyard area) were significant for log-log data ($z = -2.21$, $P = 0.03$) but not significant for semi-log data ($z = -1.00$, $P = 0.32$).

All 28 analyses (Table 2) revealed a significant species‒area relationship. The breakpoint regression model outperformed the linear model in 3 of 14 paired analyses (Table 2), thus providing statistical support for the existence of SIE in these data sets. Both the semi-log and log-log models revealed SIE in trees (Figure 2a) but not in shrubs or herbaceous plants (Figure 2b, c). We also found SIE in data of 2008 (all life forms combined), but only using the semi-log transformation. In all these analyses, the threshold area (the area below which species number does not change with patch area) was 3‒7 m^2 (Table 2). The log-log models for all study years (Figure 3) were fitted better by linear regression than by breakpoint regression (Table 2). Across all analyses, the linear and breakpoint regressions explained the species‒area relationship equally well ($F_{1, 24} = 0.06$, $P = 0.81$), and the log-log models did not differ in their performance from semi-log models ($F_{1, 24} = 1.94$, $P = 0.18$).

The similarity in species numbers between the three study years does not imply a stability of species composition. Instead, it resulted from a balance between the local extinction (minimum 119 events between 1993 and 2003 and 133 events between 2003 and 2008; Table S2) and colonisation (minimum 149 events between 1993 and 2003 and 197 events between 2003 and 2008; Table S3). The absolute turnover rate increased, whereas the relative turnover rate decreased, with an increase in open ground area (Figure 4).
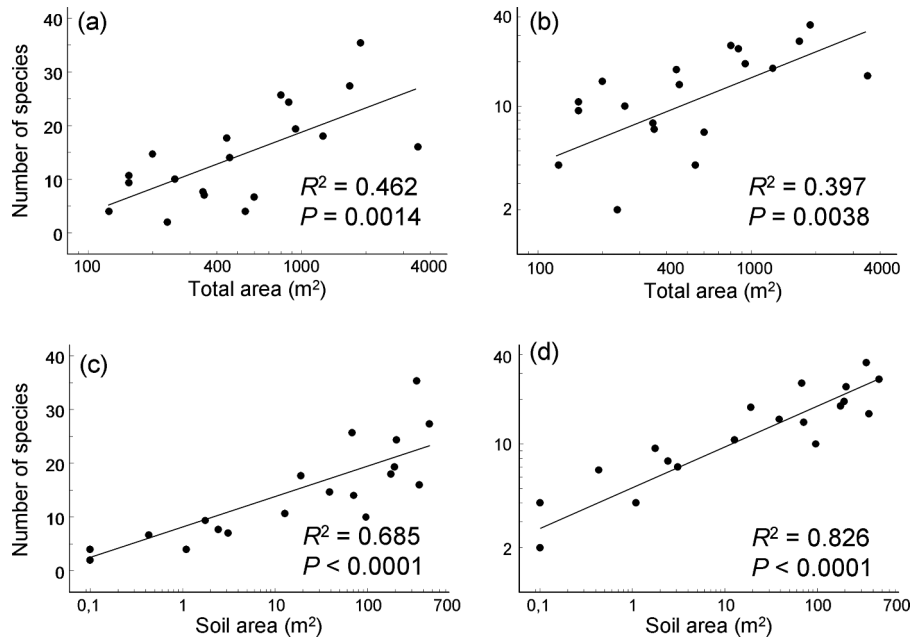
Figure 1. Relationships between the species number of native and naturalized vascular plants averaged from the surveys of 1993, 2003 and 2008 and the total courtyard area (a, b) or the area of unpaved (open) ground (c, d) for semi-log (a, c) and log-log (b, d) data.

Discussion

The vascular flora in the courtyards of central St Petersburg appeared surprisingly diverse, and it was dominated by native species. The number of species, which we recorded during three study years on an area of 14,800 m^2 (i.e. on 0.001% of the total urban area) accounted for 9.1% of the vascular flora of St Petersburg, which includes 1864 species (Belechov 2020). This high species count was primarily due to

habitat subdivision; for example, in 2003, the two largest courtyards, which contributed about 50% to the surveyed area of the open ground, jointly contained 26 plant species. By contrast, the remaining 17 courtyards jointly contained 83 species (Table 1; Data S1).

The number of plant species recorded in our courtyards increased from 80 in 1993 to 126 in 2008. We suggest that this result may be associated to three-fold

Table 2. Regression of species richness of vascular plants in courtyards of St Petersburg to the area of the open (unpaved) ground. AICc, Akaike information criterion. Within each pair, an asterisk indicates model with lower AICc.

| Data	Model type	Life form	Study year	Intercept	Slope	Threshold area, m^2	R^2	AICc
Semi-log	Linear*	All	All	7.31	6.65	.	0.70	70.04
	Breakpoint	All	All	4.44	8.10	0.97	0.72	71.82
	Linear*	All	1993	8.00	4.89	.	0.61	70.35
	Breakpoint	All	1993	3.60	6.02	0.42	0.61	73.27
	Linear*	All	2003	10.93	3.94	.	0.41	78.62
	Breakpoint	All	2003	7.40	4.52	0.29	0.42	81.77
	Linear	All	2008	8.59	8.93	.	0.78	79.19
	Breakpoint*	All	2008	3.33	15.11	3.21	0.83	77.32
	Linear	Trees	All	0.96	1.46	.	0.72	10.39
	Breakpoint*	Trees	All	0.67	2.45	4.84	0.82	4.88
	Linear*	Shrubs	All	0.72	1.06	.	0.49	16.97
	Breakpoint	Shrubs	All	0.33	1.35	1.34	0.51	19.29
	Linear*	Herbs	All	5.75	4.10	.	0.65	55.96
	Breakpoint	Herbs	All	3.56	4.71	0.60	0.65	59.08
Log-log	Linear*	All	All	0.866	0.219	.	0.84	−74.76
	Breakpoint	All	All	0.611	0.219	0.07	0.84	−71.58
	Linear*	All	1993	0.796	0.229	.	0.66	−49.97
	Breakpoint	All	1993	0.307	0.229	0.01	0.66	−46.71
	Linear*	All	2003	1.014	0.123	.	0.47	−58.11
	Breakpoint	All	2003	0.886	0.123	0.09	0.47	−54.86
	Linear*	All	2008	0.762	0.312	.	0.86	−58.40
	Breakpoint	All	2008	0.346	0.312	0.05	0.86	−55.14
	Linear	Trees	All	0.274	0.188	.	0.78	−74.09
	Breakpoint*	Trees	All	0.233	0.279	3.10	0.87	−80.03
	Linear*	Shrubs	All	0.204	0.166	.	0.63	−65.47
	Breakpoint	Shrubs	All	0.116	0.190	0.60	0.63	−61.12
	Linear*	Herbs	All	0.780	0.185	.	0.76	−71.80
	Breakpoint	Herbs	All	0.571	0.185	0.07	0.76	−65.54
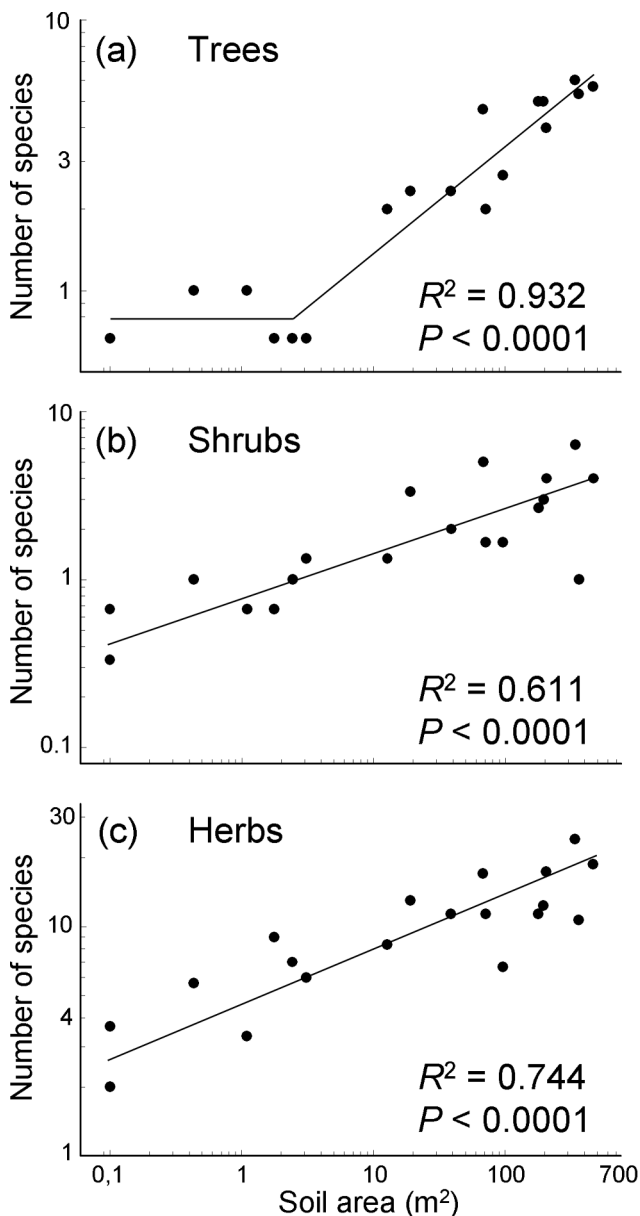
Figure 2. Relationships between the species number of native and naturalized trees (a), shrubs (b) and herbaceous plants (c) and the area of unpaved (open) ground for log-log data averaged from the surveys of 1993, 2003 and 2008. The statistics refer to the best-fit models (a, breakpoint; b, c, linear).

Figure 3. Relationships between the total species number of native and naturalized vascular plants and the area of unpaved (open) ground for log-log data from the surveys of 1993 (a), 2003 (b) and 2008 (c). The statistics refer to the best-fit (linear) models.

increase in the number of privately owned cars in St Petersburg between these years (https://rosstat.gov.ru/). The increase in the number of cars (many of which are parked in courtyards) facilitates the arrival of plant seeds from natural habitats outside the city due to direct transportation by vehicles (Ansong and Pickering 2013), as well as plant dispersal within the city, where seeds can move between courtyards due to airflow created by moving vehicles (von der Lippe et al. 2013).

The relative turnover rates (ca. 9% of species per year, on average) in our courtyards are greater than in any study system explored in this respect so far (Panitsa et al. 2008; Sarika et al. 2019; and references therein). This extreme level of turnover could be attributed to the very small size of our habitat patches
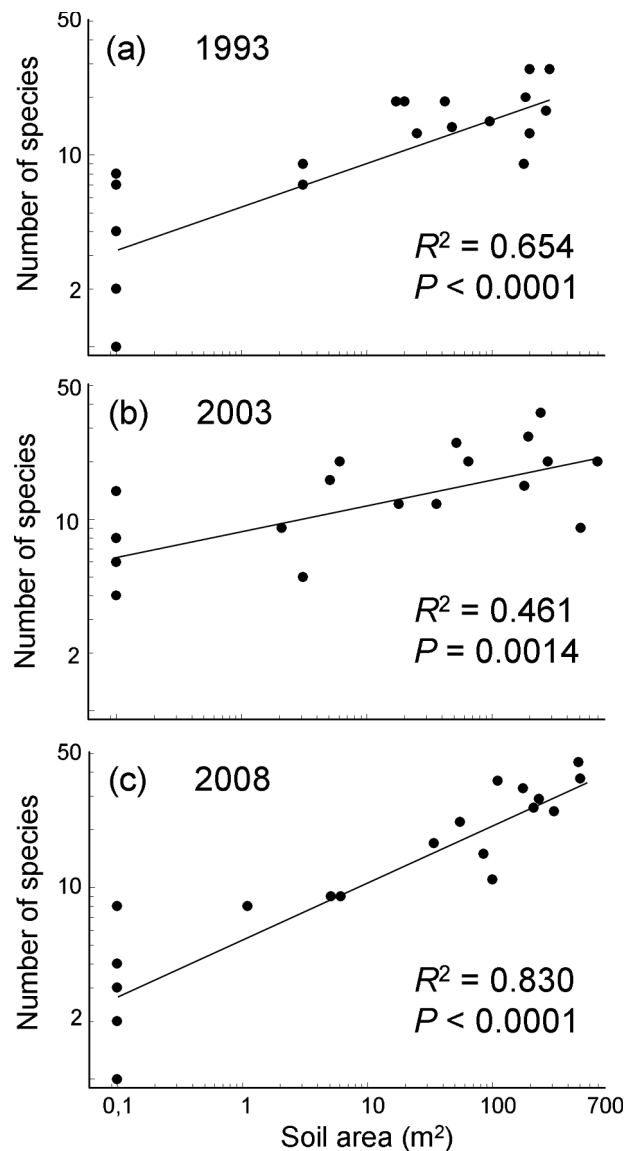
and to the high level of disturbance that was associated, for example, with cars parking inside courtyards and with the use of courtyards as children's playgrounds. Some species (e.g. *Larix sibirica* and *Malus domestica*; Table S1) were in low abundance and were represented by single individuals. The combination of low abundance, high species richness and extremely high turnover justifies both the theoretical and applied importance of analysing species–area relationships in the novel ecosystems formed in small courtyards of the historical centre of St Petersburg.

Lomolino and Weiser (2001) concluded that species richness in "small" islands and fragments generally does not depend on the island area. These authors did not specify the threshold area below which an island can be classified as small, but the lowest identified threshold area for vascular plants was 50 m^2
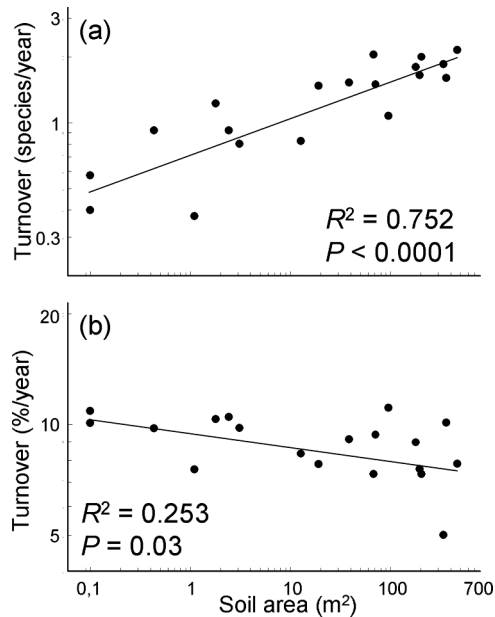
Figure 4. Relationships between the absolute (a) and relative (b) turnover of native and naturalized vascular plants and the area of unpaved (open) ground. Statistics refers to the linear models.

(islands on Lake Hjälmaren, Sweden; Lomolino and Weiser 2001). The subsequent reviews reported that the lowest threshold values in different data sets were 3000 m² (Matthews et al. 2014), 1348 m² (Wang et al. 2018; and personal communication), ca. 2500 m² (Chisholm et al. 2016) and 10,000 m² (Schrader et al. 2020). Therefore, we expected that the vascular plants inhabiting our courtyards, with the area of open ground ranking from 0.1–700 m², would show either no species-area relationship or only a slight increase in species number in the largest habitat patches.

Surprisingly, our expectations were not met. Overall, in terms of the variation explained, the linear and breakpoint regressions fitted our data equally well. However, following penalisation for the additional parameter in a segmented regression, the proportion of data sets demonstrating SIE (21%) in our study appeared much smaller than the 40-90% reported in earlier reviews (Lomolino and Weiser 2001; Matthews et al. 2014; Chisholm et al. 2016; Wang et al. 2018; Schrader et al. 2020). Intriguingly, the semi-log data on the total species richness of vascular plants was fitted by a linear model in 1993 and 2003 but by a breakpoint model in 2008, whereas the log-log data were fitted by linear models in all study years. Thus, the occurrence of SIE may well be transient and may depend on the current balance of stochastic colonisation and extinction processes, as well as on the type of data transformation (Lomolino and Weiser 2001; Matthews et al. 2014; Chen et al. 2021).

The prevalence of SIE in the species richness of trees across 17 archipelagos appeared smaller than in the total plant species richness (Schrader et al. 2020).

At the same time, we detected SIE in both semi-log and log-log data on trees, whereas no SIE was found in the total species richness. The threshold areas for trees in our data sets ranked as 3-7 m², i.e. they were one to three orders of magnitude smaller than those reported earlier (Lomolino and Weiser 2001; Matthews et al. 2014; Wang et al. 2018; Schrader et al. 2020). Mature trees were absent from all seven courtyards with areas of open ground smaller than the identified threshold area (Table S2), and the SIE was detected based on records of juvenile trees. In line with the conclusion on the higher prevalence of SIE in study systems with smaller species ranges (Chen et al. 2020), we explain the occurrence of SIE in this data set on trees by the low number of wind-dispersed tree species, which can colonise the soil accumulated in cracks in the pavement. Thus, although we found SIE in some of our data sets, we conclude that, in general, our data provide only equivocal and occasional evidence for SIE.

Our study system meets all requirements evoked by Lomolino (2000) and by Lomolino and Weiser (2001) for a set of islands/fragments that would allow SIE to emerge: courtyard areas are much smaller than the median value of the threshold area estimated by earlier studies; resource levels in individual courtyards are obviously insufficient to maintain populations of most, if not all, plant species; and episodic disturbances in courtyards are very frequent and intolerable for most plant species. We observed that the courtyard floras in central St Petersburg are completely or almost completely (with the possible exception of a few large trees) destroyed on time scales of 10 to 20 years by the renovation of pavement and on time scales of 30 to 60 years by the renovation of buildings. But even between these catastrophic disturbances, the temporal turnover in species composition is extremely high, indicating environmental instability. This instability, which could lead to independence of extinction rates from island area, and low habitat diversity, which was observed in urban courtyards, are both seen as the main drivers of SIE (Sfenthourakis and Triantis 2009; Chisholm et al. 2016). Thus, our negative, or at least inconclusive (in terms of the existence of SIE) result suggests that the conditions outlined above are not sufficient for SIE to emerge and calls for a deeper exploration of mechanisms triggering SIE in different study systems.

Our study system included both ornamental and non-ornamental plants. However, only a few courtyards had flowerbeds during one or more surveys, and these flowerbeds were generally poorly managed, i.e. they contained high numbers of spontaneously established plants of little or no aesthetic value. This poor management may explain why the explanatory power of the open ground area was much greater in our analysis ($R^2 = 0.83$; Figure 1d) than in the study of urban gardens in Sheffield, UK ($R^2 = 0.30$), where the behaviour of garden owners impacted floral

richness to a much greater extent than did garden size (Smith et al. 2006). Consistently, our analyses demonstrated that the variation in species richness did not differ between ornamental and non-ornamental plants, likely because two-thirds of the ornamental plants recorded in our courtyards have naturalized in St Petersburg (according to Byalt et al. 2019) and now establish spontaneously, like native plants. This result supports the findings of earlier studies of urban floras, which demonstrated similar species–area relationships for native and alien plants (Pyšek 1998; Smith et al. 2006). We therefore conclude that the biogeographical patterns discovered by us in native and naturalized plant species across the courtyards of St Petersburg can be directly compared with those observed in other types of habitat patches, and that the direct anthropogenic influence on species–area relationships cannot be blamed for the absence of the SIE in our study system.

The chances of a researcher to detect SIE depend on both the data quality and the research methodology. We assessed the species richness in the selected courtyards at the whole-patch scale, which is best suited for detecting SIE in plants (Schrader et al. 2019) during three study years within a 16-year long period, which gives particular weight to our data. Furthermore, two of the collectors who contributed to this assessment were blinded to the hypothesis being tested, which decreased the risk of confirmation bias – the tendency of humans to seek out evidence and interpret it in a manner that confirms their existing ideas and hypotheses (Rosenthal 1976; Nickerson 1998). We analysed the data collected from 19 fragments, each hosting 0–46 plant species; therefore, our data fit the inclusion criteria coined by Wang et al. (2018) for a global synthesis of SIE in habitat islands. Following the recommendations by Dengler (2010), our analyses included the fragments not inhabited by plants, and we accounted for model complexities while comparing the performance of the linear and breakpoint models. Thus, our result could not be attributed to a low quality of our data or to their inadequate statistical treatment.

In our study, the average slope of the log-log linear models, reflecting the rate of species accumulation with increase in open ground area, was 0.200. This value lies between the average values obtained by the global analysis of studies that have explored species–area relationships in independent sets of forested and non-forested islands or fragments (Drakare et al. 2006); that is, it did not deviate from previously analysed data sets. However, keeping in mind that species–area relationships are significantly affected by the sampling scheme, the spatial scale, and the types of organisms or habitats involved (Drakare et al. 2006), we suggest that more data sets that include very small (0.01–1000 m^2)

islets and fragments be explored in both rural and urban ecosystems to ascertain the conditions under which SIE may occur.

Conclusions

Despite the extremely small size of urban St Petersburg courtyards, their uniformity in terms of habitat diversity and extremely high temporal turnover in plant species composition, the species richness of the native and naturalized vascular plants generally increased with the open ground area. Consequently, these conditions, which are commonly seen as creating SIE, appeared insufficient for SIE to emerge in our study system. Our findings add to the growing body of evidence (e.g. Woodroffe 1986; Barrett et al. 2003; Wang et al. 2012) that SIE (in the strict sense, as defined by Lomolino and Weiser 2001) may be an exception rather than the general rule. We agree with Tjørve and Tjørve (2011) that it is premature to revise the central concept of island biogeography, and especially its conservation applications, based on the reported data on the occurrence of SIE in several study systems. From a conservation perspective, our study demonstrates that even a minor increase in the area of the open ground patches embedded in an urban matrix will increase the diversity of plants persisting in these patches. This finding justifies the importance of small actions by private individuals and by groups of citizens for maximizing the conservation of urban biodiversity and the retention of ecosystem services it provides.

Disclosure statement

No potential conflict of interest was reported by the authors.

Data availability

The data supporting the results are included in this article as supplementary file Data S1.

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