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ORIGINAL PAPER

Patterns of native and exotic species richness in the urban flora of Brussels: rejecting the 'rich get richer' model

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Abstract In this study we analyzed patterns of native and exotic species richness in the urban flora of Brussels (Belgium) using a coarse-scale systematic sampling grid of 1 km^2. The observed correlation between native and exotic richness within the grid cells sampled was then compared to the results of an adequate null model assuming no species interactions. In addition, ordinary least-squares and quantile regressions were used to analyze the relationship between the ratio of exotics to natives and the proportion of densely built up areas in each cell. Though the results obtained conform to the Eltonian expectation that exotic species preferably invade areas of low native species diversity, traditional niche-filling mechanisms seems inadequate to explain the observed pattern. Rather, aliens simply tend to have different environmental requirements than natives.

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Introduction

A number of mechanisms have been proposed that control the causes and consequences of exotic invasions (e.g., Callaway and Maron 2006; Fridley et al. 2007). Elton (1958) first hypothesized that exotic species might more easily invade species poor areas than species rich areas. This hypothesis is based on the idea that species rich areas should use limiting resources more completely, leaving fewer open niches for invaders. On the other hand, in areas of low species richness, niches are filled less completely; therefore, they are thought to have a reduced ability to repel invasions by exotics. Since then, Eltonian theory has been supported by considerable theoretical, experimental and empirical work. For thorough reviews, see Lodge (1993), Levine and D'Antonio (1999), Hector et al. (2001), Shea and Chesson (2002), Callaway and Maron (2006), and Fridley et al. (2007).

As these 'niche-filling' mechanisms operate between adjacent individuals, the hypothesis that native richness can repel invasion is best observed at the scale of local neighborhoods (Levine 2000; Shea and Chesson 2002) such that available experimental research (e.g., Tilman 1997; Hector et al. 2001;

Kennedy et al. 2002) and observational studies (Brown and Peet 2003) that corroborate this hypothesis were usually performed at rather small scales.

On the other hand, at coarser scales, the observed correlation between native and exotic species richness is usually positive (e.g., Stohlgren et al. 1999, 2002, 2003; Sax 2002; Deutschewitz et al. 2003). This effect is usually known as the 'rich-get-richer' model, and is often presented as evidence that, while at finer scales native richness can repel invasion via niche partitioning and competitive exclusion, at scales larger than local neighborhoods variation in resource availability (Stohlgren et al. 2002; Kalkhan and Stohlgren 2000; Shea and Chesson 2002), propagule supply (Levine 2000; Brown and Peet 2003) or facilitation mechanisms as diverse as habitat amelioration or protection from pests or predators (Richardson et al. 2000; Bruno et al. 2003) are more important drivers of exogenous immigration (see Fridley et al. 2004).

Nonetheless, as emphasized by Fridley et al. (2004), the observed change in the relationship between native richness and invasion success with scale is usually a statistical artifact that is due to the misuse of inadequate null models rather than to genuine ecological driving forces. Contrary to the common assumption that the null expectation of the native-exotic richness relationship is a flat regression line with a slope close to zero, randomly assembled communities of native and exotic species display scale-dependent emergent patterns. For instance, given coarse-scale random community assembly, species rich plots are more likely to include more natives and exotics regardless of the mix of natives or exotics. This pattern usually results in a positive correlation between native and exotic richness. By contrast, at finer scales, constraints on total species richness within each plot may artificially produce negative native-exotic correlations that may be interpreted as the result of ecological mechanisms that progressively repel invasion with increasing native richness (Fridley et al. 2004). Accordingly, to correctly test theoretical assumptions on invasion mechanisms, observational data on native-exotic relationships must be compared to appropriate null expectations.

In this paper we analyzed patterns of native and exotic species richness in the urban flora of Brussels (Belgium) using a coarse-scale systematic sampling grid of 1 km^2. The relationship between the observed native and exotic richness was compared to the results of an adequate null model proposed by Fridley et al. (2004) assuming no species interactions.

Methods

Study area

The city of Brussels covers an area of roughly 161 km^2. It is characterized by a temperate climate with mean annual temperature of 9.9°C and mean annual rainfall of 798 mm. There are approximately 1 million inhabitants in Brussels and, from a structural point of view, it appears as a succession of four concentric zones, from its business and historical center to the outlying suburbs (IBGE-BIM 1995): (1) the core is dominated by commercial and administrative activities with a limited residential function; (2) the districts, constructed in the last century, are densely built up; (3) the periphery, less densely built up; (4) the suburbs which can be considered as the peak demographic growth zone. This part of the city still keeps relatively rural enclosures.

Data collection

For sampling the urban flora, we used a systematic grid covering the whole city of Brussels. The study area included 159 grid cells of 1 km^2 that are included in the administrative limits of the city for at least 75%. Within each of these 1 km^2-cells, all presences of spontaneous seed plants (spermatophytae) were recorded during 3 years 1992–1994 from March to October, wherever they occurred within the administrative limits of the city, systematically avoiding those species that were obviously planted. Except private gardens, the whole city area has been prospected, including managed areas (e.g., parks and lawns). In order to avoid undersampling because of the seasonal variation, each 1 km^2-cell was surveyed twice along the growing season (early spring and summer or early autumn). For each visit, the duration of search was long enough to reach the point where further sampling did not allow to add further species to the list. In recent years, the species inventory has been constantly updated and currently totals 671 spontaneously occurring seed species with at least one spatially explicit record within the sampling grid. Species were then divided according to their status into native species (species that are native to the region of Brussels; 518 species) and alien species (153 species).

Statistical analysis

To analyze the relationship between native and exotic richness in Brussels, we counted the number of native and exotic species within each 1 km^2-cell and calculated the correlation coefficient (r) and the slope (s) of the ordinary least-squares (OLS) regression line. We then compared the observed values to a distribution of similarly calculated values from 999 permutations in which we randomly reassigned 'native' and 'exotic' labels to each out of the 671 species in the species pool of Brussels. In this way, we generated artificial species assemblages that were assembled at random with respect to the composition of native and exotics, keeping constant the total species richness of each sample quadrat together with the total number of native and exotics in the species pool. For randomization we used the program PopTools, a free Excel add-in available on the Internet at: http://www.cse.csiro.au/poptools. *P*-values (one-tailed test) were computed as the proportion of randomly derived values that were as extreme or more extreme than the actual values (see Fridley et al. 2004).

We also fitted linear models using both OLS and quantile regressions to analyze the relationship between the ratio of exotics to natives (ENR) and the proportion of densely built up areas in each cell. The distribution of densely built up areas in Brussels was extracted from the biological evaluation map at scale 1:10000 (Brichau et al. 2000), which is a standardized field survey and evaluation of the biotic environment of Flanders and the Brussels capital region.

Quantile regression (Koenker and Bassett 1978; Koenker and Hallock 2001) seeks to complement classical linear regression analysis to estimating all parts of the response distribution conditional on the predictor variable, thus providing a more comprehensive characterization of the effects than those provided by estimates of the conditional mean as made with OLS regression (Cade and Noon 2003). Quantile-based fitting gives different weights to positive and negative residuals, leading to an asymmetric minimization. Let $\{\rho_1, \rho_2, \ldots, \rho_\mathrm{n}\}$ denote the values of the ratio of ENR lying within the scatterplot of ENR versus the proportion of densely built up areas. OLS regression minimizes residuals by solving

$$\text{Residual} = \min \sum (\rho_i - \hat{\rho}_i)^2 \tag{1}$$

where $\hat{\rho}_i$ is the estimated value for each ρ_i. Quantile regression gives different weights to positive and negative residuals and considers absolute rather than squared residuals, such that

$$\text{Residual} = \min \sum |\rho_i - \hat{\rho}_i| T \tag{2}$$

where T is a multiplier term that is equal to τ (the quantile value) for positive deviations (i.e., $(\rho_i - \hat{\rho}_i) > 0$) and to $1 - \tau$ for negative deviations. This asymmetric minimization fits a regression model through the upper part of the response distribution for $\tau > 0.5$ and through the lower part of the distribution for $\tau < 0.5$. For $\tau = 0.5$ we obtain the median regression, which can be used as a central regression line similar to the mean regression estimated with OLS regression. Quantile regression overcomes thereby various problems that OLS is confronted with. For instance, by focusing on the mean, information about the tails of a distribution is lost. Also, OLS is rather sensitive to extreme outliers, which can distort the results significantly. By contrast, being based on absolute values rather than on squared deviations, quantile regression reduces outlier effects.

In this paper, to emphasize the behavior of maximum values of ENR conditional to the proportion of densely built up areas, upper quantile thresholds were considered. We used the 'quantreg' package of R-software (Koenker 2007); confidence intervals for quantile regression estimates were based on the rank-score test inversion approach with a localized bandwidth of quantiles, providing weights to account for distributional heterogeneity (see Cade et al. 2005).

Results

The observed correlation between native and exotic richness within the 159 cells of the urban flora of Brussels is shown in Fig. 1. Native and exotic species richness were positively correlated ($r = 0.860$,

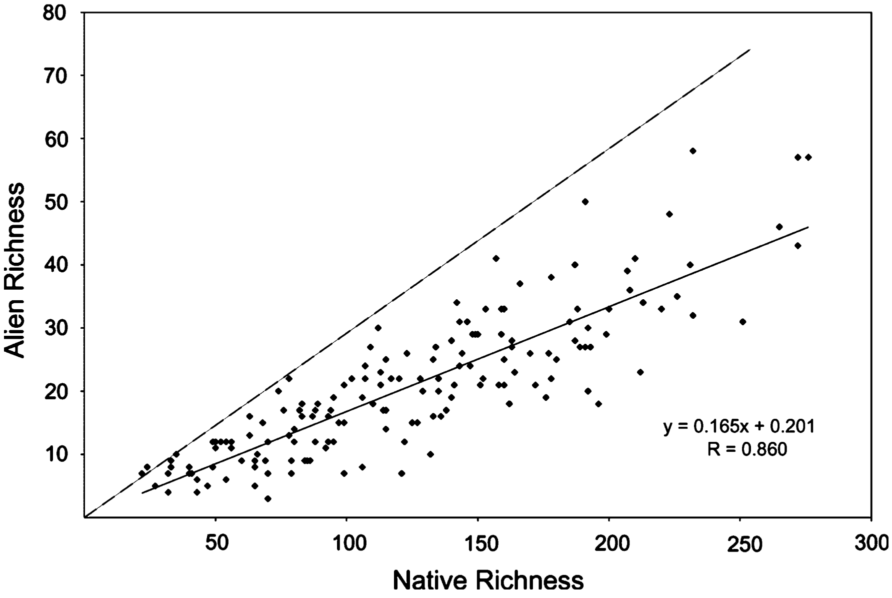

Fig. 1 Relationship between native and alien species richness observed within the 159 grid cells of 1 km^2 in size used for sampling the urban flora of Brussels. The *dotted line* is the mean slope of the 999 random least-squares regressions $s = 0.291$. This value is very close to the ratio of exotics to natives in the species pool (i.e., for Brussels, 153/518 $\approx$ 0.295)

Table 1 Observed and random values obtained from the regression between native and alien species richness in the urban flora of Brussels

	r	Slope
Observed values	0.860***	0.165***
Mean random values	0.967	0.291
Minimum random values	0.931	0.220
Maximum random values	0.981	0.367

*** $P = 0.001$ (one-tailed test)

$s = 0.165$). However, surprisingly, the correlation coefficients and the slopes of the 999 OLS regressions obtained under a null model of a randomly assembled set of native and exotic species were always higher than the observed values, with null values of r varying from 0.931 to 0.981 (mean $r = 0.967$) and null values of s in the range 0.219–0.367 (mean $s = 0.291$; see Table 1). Therefore, if the scale-dependent statistical constraints implied in the random null model are correctly considered, for both test statistics the most extreme level of significance possible $P = 0.001$ (i.e., 1 in 1,000) were obtained meaning that, for our Brussels data, the regression between native and exotic species richness is significantly worse than expected by a random null model.

As shown in Table 2, the slopes of both OLS and quantile regressions of ENR versus the degree of densely built up areas in each cell were all statistically significant ($P < 0.01$), meaning that the ratio of exotic to native species increases with increasing levels of densely built up areas in the cells sampled (Fig. 2). Also, the higher rates of increase associated to the quantile regressions denote that the maximum values of ENR raise more steeply with increasing proportions of densely built up areas than the mean rate of increase estimated by OLS regression.

Table 2 Linear regression models summarizing the increase of the ratio of exotics to natives (ENR) with increasing proportions of densely built up areas

Regression type	τ	Slope $\times 10^{-4}$	Slope boundaries $\times 10^{-4}$ (CI 99%)
OLS	–	5.1**	2.5–7.7
Quantile	0.75	5.7**	1.8–9.0
	0.90	7.1**	2.4–14.1
	0.95	8.8**	2.3–13.0

OLS ordinary least-squares regression, *CI* confidence interval, ** $P < 0.01$

Discussion

According to Gotelli and Graves (1996), a null model operates as a standard statistical null hypothesis for detecting pattern that would be expected in the absence of a particular ecological mechanism. By shuffling native-exotic labels within the urban species pool, keeping the total richness and actual species

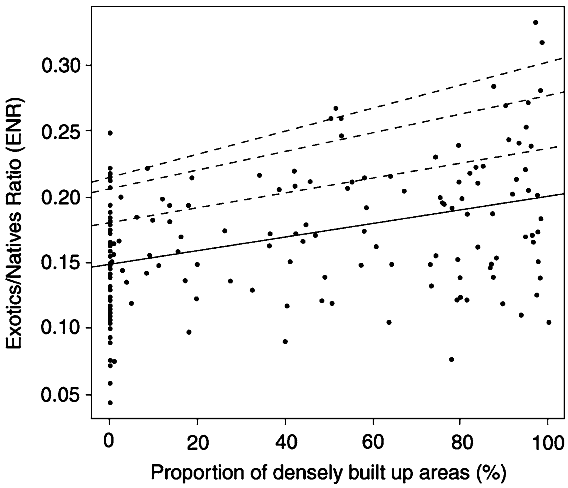

Fig. 2 Increase of ENR versus the proportion of densely built up areas in each cell sampled. OLS (*solid line*) and quantile regressions (*dashed lines*) considering *three* different values of τ (*from upper to lower lines*: 0.95, 0.90, 0.75)

composition of each 1 km^2-cell constant, our null model allowed us to isolate the statistical constraints on native and exotic richness patterns in real species assemblages of given spatial resolution (Fridley et al. 2004). As a result, though coarse-scale native and exotic species richness of Brussels were positively correlated, the correlation coefficient and the slope of the observed least-squares regression are both significantly lower than the results obtained from a random null model (see Fig. 1). That is, the observed degree of correlation between native and exotic richness is actually much weaker than expected by chance conforming to the Eltonian expectation that exotic species preferably invade areas of low native species diversity. Particularly, as observed by Fridley et al. (2004) at coarser scales, the expected slope of the least-squares regression is defined by the ratio of ENR in the species pool (i.e., for Brussels, 153/518 $\approx$ 0.295). The finding that the observed slope of the regression line is much lower than the expected slope from the null model means that exotic species are under-represented in the total dataset as compared to native species. For instance, though the occupancy frequency distributions of the native and exotic plants of Brussels are both unimodal with a satellite mode (sensu McGeoch and Gaston 2002; Fig. 3), native species are found on average in 38.25 cells, while the mean cell occupancy of the exotic species is only 21.69 cells.

From an ecological viewpoint, this significantly lower-than-random correlation between native and exotic richness is most likely not connected to the niche-filling mechanisms hypothesized by Elton (1958). More probably, as it is the case for most urban areas, Brussels aliens possess different environmental requirements than natives: alien species tend to occur in well-lit, dry, nitrogen-rich, alkaline and warm places (Godefroid 2001). Their higher temperature and aridity requirements can be better met in the city center where the urban heat-island effect is more pronounced (Sukopp and Werner 1983; Gilbert 1989), while native richness is usually limited. These requirements reflect their origin in warmer regions (i.e., the Mediterranean basin for most Brassicaceae and North America or Asia for Poaceae). In Brussels, 34% of the alien species originate from Asia, 34% from south Europe, 16% from Africa, and 16% from America (Godefroid 1996).

Also, while native species have their major diaspore sources in natural areas (see Celesti-Grapow et al. 2006), aliens are often dependent on humans as far as dispersal is concerned such that more natural, peripheral sites richer in natives may be less favorable for survival. As cities are the main centers of their introduction, aliens are usually over-represented in the city center compared to more peripheral zones or the surrounding landscape (Godefroid 2001; Chocholoušková and Pyšek 2003; Kühn et al. 2004). Pyšek (1998) found that the number of alien species in rural villages of Bohemia was, beside the village size and altitude, negatively related to the distance from the nearest medium-sized town, while Celesti-Grapow et al. (2006) found that in the city of Rome (Italy) aliens were most represented in the historical center which has the lowest species richness and the highest levels of disturbance. In Brussels, Godefroid (2001) confirmed that aliens are better represented in the city center. Land use, and in particular building densification in already built up areas is the main driver of plant species composition in Brussels: there is a strong positive relationship between densely built up areas and the presence of aliens (Godefroid and Koedam 2007) such that the proportion of non-native species can be used as an indicator for the intensity of disturbances caused by human activities.

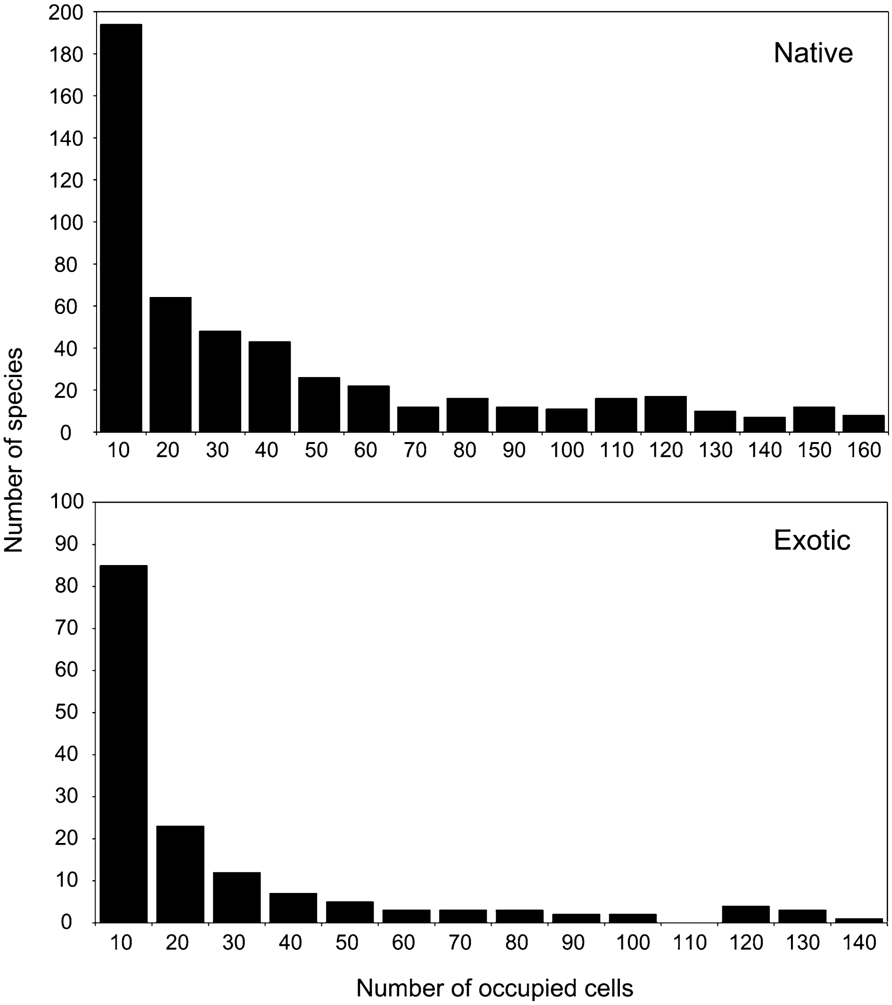

Fig. 3 Frequency distribution of occupied cells for the native (518 species) and exotic (153) plant species of Brussels

The positive relationship between densely built up areas and the presence of aliens is supported by the significant results of OLS and quantile regressions with all τ values. That is, densely built up areas offer a more favorable environment to exotics, such that the local proportion of exotic species in the urban flora increases with increasing levels of urbanization. OLS regression estimate of mean increase rate of ENR versus densely built up areas is less than two-thirds of the rate of increase shown by the upper quantiles (Table 2) meaning that, given the same increase in urbanization, ENR maxima will increase much faster as compared to the ENR mean. In this view, densely built up areas represent a direct effect particularly on the maximum values of ENR. Fitting a regression model through the upper part of the response distribution, quantile regression revealed a trend which may underestimated by OLS (see Cade et al. 2005).

Overall, our results suggest that the patterns of native and exotic richness in Brussels are very close to those expected by Eltonian theory. However, these patterns seem to be driven by niche differentiation between native and exotics rather than by niche-filling mechanisms and community saturation effects. Is this a general feature of urban communities? This is a critical question, and its answer may provide valuable insights into the spatial component of invasion dynamics.

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