

Invasiveness of alien plants in Brussels is related to their phylogenetic similarity to native species

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ABSTRACT

Aim Understanding the processes that drive invasion success of alien species has received considerable attention in current ecological research. From an evolutionary point of view, many studies have shown that the phylogenetic similarity between the invader species and the members of the native community may be an important aspect of invasiveness. In this study, using a coarse-scale systematic sampling grid of 1 km², we explore whether the occupancy frequency of two groups of alien species, archaeophytes and neophytes, in the urban angiosperm flora of Brussels is influenced by their phylogenetic relatedness to native species.

Location The city of Brussels (Belgium).

Methods We used ordinary least-squares regressions and quantile regressions for analysing the relationship between the occupancy frequency of alien species in the sampled grid and their phylogenetic distance to the native species pool.

Results Alien species with high occupancy frequency in the sampled grid are, on average, more phylogenetically related to native species than are less frequent aliens, although this relationship is significant only for archaeophytes. In addition, as shown by the quantile regressions, the relationship between phylogenetic relatedness to the native flora and occupancy frequency is much stronger for the most frequent aliens than for rare aliens.

Main conclusions Our data suggest that it is unlikely that species with very low phylogenetic relatedness to natives will become successful invaders with very high distribution in the area studied. To the contrary, under future climate warming scenarios, present-day urban aliens of high occupancy frequency are likely to become successful invaders even outside urban areas.

Keywords

Archaeophytes, biological invasions, neophytes, phylogenetic distance, quantile regression, randomization.

INTRODUCTION

Increasing globalization and human mobility have facilitated the intentional and unintentional introduction of species beyond their natural geographic ranges. Such alien species are considered to be a main driver of global biodiversity loss with substantial environmental and economic impacts on invaded communities. While the potential economic cost for almost 90% of the alien species found in Europe is still unknown, the European Commission (2008) estimated the economic impact of alien species in Europe to be close to €10 billion annually,

giving urgency to the scientific community to better understand which species are likely to have large impacts on the novel communities to which they are introduced.

In this framework, urban areas usually contain the greatest proportion of alien plants; on one hand, cities act as focal point for the broad-scale introduction (both intentional and unintentional) of new species (Pyšek, 1998; Wittig, 2004; Chytrý *et al.*, 2005, 2008). On the other hand, the ‘urban heat-island effect’ provides distinctive environmental conditions that have allowed many alien species with higher temperature requirements and tolerance for arid environments to become

established in urban environments (Sukopp & Werner, 1983; Godefroid & Koedam, 2007). Thus, for studying the ecology of biological invasions, urban vascular floras are an informative focal group (McKinney, 2006; LaSorte *et al.*, 2008; Ricotta *et al.*, 2009).

Besides accidental factors, the invasion success of a species depends on traits associated with the ability to reproduce and disperse (Pyšek & Richardson, 2007), compete with resident vegetation (Daehler, 2003; Vilà & Weiner, 2004), accommodate and allocate resources or tolerate stressful factors (McDougall *et al.*, 2006; Muth & Pigliucci, 2007). These traits result on one hand from adaptation strategies in the invaded range and, on the other hand, from the long-term evolutionary history of the alien species in their native ranges. Therefore, it is likely that alien species with different traits differ in their invasion success of a given habitat.

From an evolutionary perspective, functionally related species that coexist in the same habitat often share a common phylogenetic history, such that phylogenetic relatedness is expected to correlate to some extent with ecological similarity (Webb *et al.*, 2002; Donoghue, 2008). It is usually assumed that, because of limiting similarity due to overlap in resource use, phenotypic and phylogenetic relatedness between native and alien species reduces the success of invasion (Darwin's naturalization hypothesis; see, e.g. Daehler, 2001). In support of the proposed pattern, Strauss *et al.* (2006) found that highly invasive grass species are, on average, significantly less related to native grasses than expected from a random sampling of the phylogenetic supertree of all grass species of California. This is in agreement with previous studies of Rejmánek (1996), who found that European grasses from alien genera were over-represented in California's naturalized flora.

At coarser spatial scales where plant-to-plant competitive interactions become irrelevant, it has been suggested that alien species more closely related to natives are more likely to succeed because they are expected to share traits that pre-adapt them to their new environment (Swenson *et al.*, 2007; Diez *et al.*, 2009). The idea that phylogenetic similarity between native and alien species may favour coarse-scale invasion success is supported by work showing that, especially in urban environments, environmental filters and phylogenetic clustering are major drivers of community assembly (see Webb *et al.*, 2002; Vamوسي *et al.*, 2009). Using data from 21 urban floras located in Europe and eight in the United States of America, Ricotta *et al.* (2009) showed that the phylogenetic diversity of alien species is significantly lower than that of native species, both at the continental scale and at the scale of single cities. Knapp *et al.* (2008a) compared the phylogenetic diversity of urbanized areas in Germany with those of rural areas. Their results show that the higher species richness of urban areas is usually due to taxonomically and functionally related species that are adapted to disturbances associated with human pressure. Importantly, coarse-scale phylogenetic attraction and small-scale phylogenetic repulsion (predicted by Darwin's naturalization hypothesis) are not mutually exclusive; rather,

support for both processes might be found in the same study area, but on different spatial scales. For a review on scale-dependency of phylogenetic patterns in biological invasions, see Procheş *et al.* (2008).

Unfortunately, most of the articles that analyse the mechanisms of urban alien invasions are based on species presence and absence data only. Nonetheless, as stressed by Strauss *et al.* (2006), there is a basic distinction between unsuccessful invaders with a low ability to spread that form small populations of a few individuals and high-impact invaders that become dominant or co-dominant species and severely affect the invaded habitat. Accordingly, in this article, we ask whether the coarse-scale distribution of alien species in the urban angiosperm flora of Brussels (Belgium) is influenced by their phylogenetic relatedness to native species. We also ask whether there is a difference in phylogenetic patterns shown by two groups of alien species: archaeophytes, which arrived before AD 1500, and neophytes, which arrived after that date (Pyšek *et al.*, 2004; Pyšek & Jarošík, 2005; see later for further explanation on the main differences between archaeophytes and neophytes). Our working hypothesis is that the longer residence times of archaeophytes together with their more restricted regions of origin and habitats will lead to tighter phylogenetic relationships to native species when compared to neophytes.

STUDY AREA

The city of Brussels hosts approximately 1 million inhabitants and covers an area of roughly 161 km². The urban landscape is extremely complex and stratified as in any area of long-standing settlement, while the superimposition of different historical periods severely affects the urban distribution of vegetated areas and plant species richness.

Brussels has a temperate climate with mean annual temperature of 9.9°C and mean annual rainfall of 798 mm. The flora of Brussels was comprehensively surveyed from 1992 to 1994. All spontaneous (naturally growing) plants were recorded within a grid composed of 189 cells of 1 km², systematically avoiding those species that were found planted but not naturalized (IBGE, 1999). In the framework of this study, only those grid cells that are included in the administrative limits of the city for at least 75% were considered. The species inventory totals 674 Angiosperms, which were then divided according to their status into native species (species that are native to the region of Brussels; 488 species), archaeophytes (57 species) and neophytes (129 species).

Archaeophytes are alien species introduced into Europe prior to AD 1500, mostly from the Mediterranean Basin, and are usually weeds of arable land. Neophytes were introduced into Europe after the discovery of the New World, signifying the beginning of relatively rapid and substantial changes in human movement, demography, agriculture, commerce and industry (Ricotta *et al.*, 2009). The distinction between these two groups of alien species, which is widely used in Central-

European phytogeographical studies (see Pyšek, 1995; Pyšek *et al.*, 2002), is important within the context of this study, as we hypothesize that different invasion histories and residence times will affect the strength of the relationship between the coarse-scale occupancy frequency of alien species in the urban flora of Brussels and their phylogenetic relatedness to native species.

METHODS

Data analysis

We constructed a phylogenetic tree for the flowering plants (Angiospermae) of Brussels using the Phylomatic online software, a tool for the construction of phylogenetic relationships among taxa freely available at <http://www.phylodiversity.net/phylomatic> (Webb & Donoghue, 2005). The tree is based on the highly resolved base tree of the Angiosperm Phylogeny Group (APG 2003) in combination with recently published family phylogenies. Tree nodes are dated according to Wikstrom *et al.* (2001).

To compare the degree to which neophytes and archaeophytes are phylogenetically related to natives, we used two different metrics: the phylogenetic distance of each alien species to its nearest relative in the native flora (NNPD), and the mean phylogenetic distance (MPD) separating each alien species from the whole native flora (Webb, 2000). The phylogenetic distance between two species is the total branch length separating those species. For an aged ultrametric tree, this will be twice the time since divergence (in Myr) from the most recent common ancestor (branch length from species 1 to the most recent common ancestor plus branch length from the most recent common ancestor to species 2).

MPD was calculated both as unweighted mean of phylogenetic distances of each alien species from all native species and weighting each distance by the occupancy frequency of the corresponding native species in the sampled cells. While MPD summarizes the degree of (weighted or unweighted) 'phylogenetic uniqueness' of a given alien species with respect to the overall native flora, NNPD addresses whether phylogenetic similarity to the closest native species has important effects on invasiveness.

Next, we analysed the relationship between MPD and NNPD values of both alien species groups and their occupancy frequency in the sampled grid fitting linear models using both ordinary least-squares (OLS) and quantile regressions.

Although a number of different measures of species distribution or commonness can be found in the ecological literature (for a review see Gaston, 1994), in this article, we equate species commonness with the species occupancy frequencies (SOFs) in the sampled grid (see Ricotta *et al.*, 2008). This approach is particularly adequate at coarse spatial scales where data on species abundances are generally unknown. Also, focusing on invasion problems, the comparison of species abundances is largely meaningless between individuals with different growth forms such as herbs and

trees, while the species coarse-scale spatial distribution may be reasonably assumed as an estimator of their ability to spread through the invaded region. As SOFs are bounded on both sides, for statistical analysis, the data were logit transformed according to the usual formula $\text{logit}(p) = \log[p/(1-p)]$, where p is the proportion of occupied cells with respect to the right hand bound of the distribution (see, e.g. Williamson & Gaston, 1999).

Quantile regression (Koenker & Bassett, 1978; Koenker & Hallock, 2001) seeks to complement classical linear regression analysis by estimating all parts of the response distribution conditional on the predictor variable, thus providing a more comprehensive characterization of the effects than that provided by estimates of the conditional mean as made with OLS regression (Cade & Noon, 2003). Quantile-based fitting gives different weights to positive and negative residuals, leading to an asymmetric minimization. Let $\{\rho_1, \rho_2, \dots, \rho_n\}$ denote the values of all SOFs lying within the scatter plot of MPD (or NNPD) versus the logit-transformed SOFs in the sampled grid. OLS regression minimizes residuals by solving

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

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

$$\text{residual} = \min \sum |\rho_i - \hat{\rho}_i|T \quad (2)$$

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 regression is confronted with. For instance, by focusing on the mean, information about the tails of a distribution is lost. Also, OLS regression 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 (Gotelli & Ellison, 2004). In this article, to emphasize the behaviour of the SOFs in the sampled grid conditional to the maximum values of phylogenetic distances, upper quantile thresholds with $\tau = 0.75$ and $\tau = 0.90$ were considered. We used the 'quantreg' package of R-software (Koenker, 2009). Statistical significance for quantile regression estimates was tested using the bootstrap test procedure implemented into the R package. For mathematical details, see Koenker (1994) and Bose & Chatterjee (2003). Statistical significance for OLS regressions was tested using a randomization test in which the occupancy frequency values of archaeophytes and neophytes were randomly shuffled across species (see Manly, 2007). In both cases 9999 random iterations were used.

RESULTS

The results of the OLS and quantile regressions on MPD and NNPD versus the occupancy frequency of archaeophytes and neophytes are shown in Table 1. The OLS regressions show a significantly negative relationship ($P < 0.05$) between the phylogenetic distance of archaeophytes from the native flora and their coarse-scale occupancy frequency in the sampled grid. However, the variance explained by the regression between the index NNPD and the SOFs of archaeophytes ($R^2 = 0.113$) is roughly twice the variance explained by the weighted and unweighted versions of the index MPD ($R^2 = 0.048$ and 0.057 , respectively), denoting that, for our logit-transformed data set, phylogenetic similarity to the closest native seems more important than mean phylogenetic similarity to the overall native flora in shaping the invasion pattern of archaeophytes. Also, for archaeophytes, the steeper slopes associated with the quantile regressions when compared to the OLS regression indicate that the maximum values of species commonness decrease more rapidly with increasing phylogenetic distance from the native species than the mean rate of decrease estimated by OLS regression (see Fig. 1). That is, given the same decrease in the species phylogenetic metrics, the maximum values of the logit-transformed SOFs will decrease much faster when compared to the corresponding mean. In this view, the slopes of the quantile regressions obtained using the weighted version of the index MPD are qualitatively similar to those obtained from the unweighted MPD, meaning that, at least in our case, weighting the mean phylogenetic similarity of aliens by the SOFs of natives does not influence the sign and the strength of the relationship between the mean phylogenetic similarity of aliens to natives and their occupancy frequencies.

The same behaviour (i.e. the steeper regression slopes are associated with the highest quantile values) is found for the neophytic flora. However, for neophytes, the sole (marginally)

significant regressions at $P < 0.1$ are the quantile regressions with $\tau = 0.90$. This means that for neophytes, only the most common species (i.e. those species with very high values of occupancy frequency in the sampled grid) show some significant degree of phylogenetic relatedness to the native flora of Brussels.

DISCUSSION

Phylogenetic relationships between species are usually assumed as a good indicator of their degree of evolutionary and ecological relationships, thus allowing for the integration of phylogenetic information into studies of species assembly (Webb *et al.*, 2002). Thompson *et al.* (1995) noted that ecological attributes of successful aliens are strongly habitat dependent and that most of them are shared by successful native species. Likewise, Knapp *et al.* (2008b) showed that the floras of urbanized and rural areas in Germany showed clear differences in the proportion of their functional trait states. According to Knapp *et al.* (2008b), urbanized areas have higher proportions of wind-pollinated plants, plants with scleromorphic leaves or plants dispersed by animals, and lower proportions of insect-pollinated plants, plants with hygromorphic leaves or plants dispersed by wind than rural areas.

At the same time, urbanization creates physical conditions allowing the establishment of alien species outside their natural habitat. In Brussels, most alien species tend to occur in well-lit, dry, nitrogen-rich, alkaline and warm places (Godefroid, 2001; Godefroid & Koedam, 2007). These higher temperature and aridity requirements, which reflect the origin of most Brussels aliens in warmer regions (i.e. the Mediterranean Basin for most Brassicaceae and North America or Asia for Poaceae; Godefroid, 1996), can be better met in the city centre where the urban heat-island effect is more pronounced (Sukopp & Werner, 1983), while the pH values of many urban soils are increased by adjacent concrete and other lime-based materials

Phylogenetic metric	Regression type		Slope	
			Archaeophytes	Neophytes
Unweighted MPD	OLS		-0.014* ($R^2 = 0.057$)	-0.004 ($R^2 = 0.007$)
	Quantile	$\tau = 0.75$	-0.021*	-0.004
		$\tau = 0.90$	-0.024*	-0.008 ^{MS}
Weighted MPD	OLS		-0.011* ($R^2 = 0.048$)	-0.003 ($R^2 = 0.007$)
	Quantile	$\tau = 0.75$	-0.019*	-0.003
		$\tau = 0.90$	-0.022*	-0.008 ^{MS}
NNPD	OLS		-0.010* ($R^2 = 0.113$)	-0.002 ($R^2 = 0.007$)
	Quantile	$\tau = 0.75$	-0.011*	-0.003
		$\tau = 0.90$	-0.016*	-0.007 ^{MS}

OLS, ordinary least-squares regression; MPD, mean phylogenetic distance; NNPD, nearest neighbour phylogenetic distance; τ , quantile value, * $P < 0.05$, MS, marginally significant at $P < 0.1$.

Table 1 Linear regression models summarizing the relationship between phylogenetic distances of archaeophytes and neophytes from native species and their logit-transformed occupancy frequency in the sampled grid. For OLS regressions, the coefficient of determination R^2 is also shown.

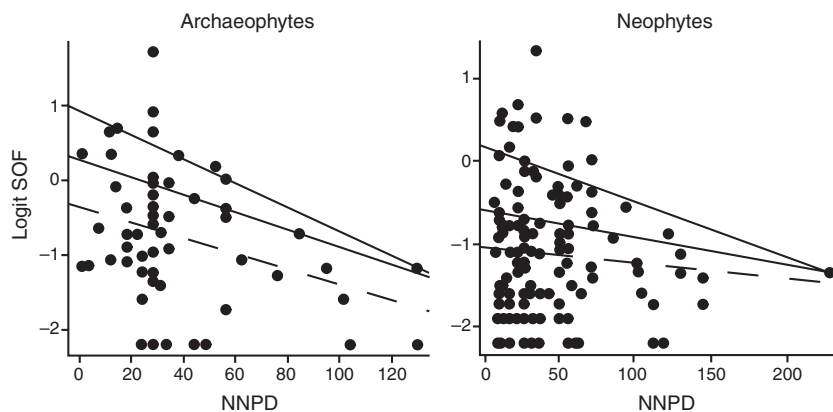


Figure 1 Plots of the logit-transformed species occupancy frequencies (SOFs) of archaeophytes and neophytes in the sampled grid of Brussels versus NNPD. Ordinary least-squares (dashed line) and quantile regressions (solid lines) considering two different quantile values (from upper to lower lines: $\tau = 0.90$ and $\tau = 0.75$). Note that the presence of the outlier *Parthenocissus inserta* on the right-side of the second plot does not change the sign and the strength of the observed relationships between the logit-transformed SOFs of neophytes and NNPD.

(Sukopp, 2004; Godefroid *et al.*, 2007; Thompson & McCarthy, 2008). As functional traits are usually conserved through evolutionary history (Donoghue, 2008), alien species with high phylogenetic relatedness to natives are more likely to share those well-suited traits, which enable them to succeed (Procheş *et al.*, 2008).

Overall, our analysis shows that the coarse-scale SOFs of archaeophytes in the urban angiosperm flora of Brussels is weakly, though significantly, influenced by their phylogenetic relatedness to native species, such that common archaeophytes are on average phylogenetically closer to native species when compared to rare archaeophytes. As shown by the quantile regressions, this phylogenetic relatedness to the native flora is particularly evident for the most common species. That is, for archaeophytes, phylogenetic relatedness represents a direct effect particularly on the maximum values of occupancy frequency, such that quantile regression on the upper part of the response distribution revealed a trend which is underestimated by OLS (see Cade *et al.*, 2005; Rocchini & Cade, 2008). The same general pattern is also observed for neophytes, though in this case, only the quantile regressions with $\tau = 0.90$ are marginally significant at $P < 0.1$. These observations support the assumption that, at this scale of analysis, pre-adaptation to the environmental conditions proper of the urban areas is an important mechanism in driving the species ability to spread. As shown in Fig. 1, no alien species is at the same time both very frequent and taxonomically very dissimilar from natives. Nonetheless, although pre-adaptation to urban environmental conditions is a relevant step in the invasion process, alone it does not ensure the species invasion success. For instance, rare aliens, which are by definition unsuccessful invaders, could be highly pre-adapted to the environmental conditions of urban habitats, they might just lack the dispersal potential or the human-induced propagule pressure that promote the spread of the frequent aliens. This might be one reason for the low proportion of variance explained by the OLS regressions between the SOFs of alien species and their phylogenetic relatedness to native species.

Accordingly, for the most common aliens (the upper quantiles), it is more likely that pre-adaptation to environmental conditions is the dominant constraint for their general ability to spread, while rare species might predominantly be constrained by dispersal limitation (and therefore do not show a significant relationship between phylogenetic relatedness and frequency).

In this context, the stronger relationship between phylogenetic relatedness and occupancy frequency of archaeophytes is probably related to the different invasion history of archaeophytes in comparison to that of neophytes. The two groups of alien species differ in the region of origin and habitat specificity, which is more diverse for neophytes (Lambdon *et al.*, 2008), while the majority of archaeophytes were typically weeds of arable land (Pyšek *et al.*, 2005). Another primary difference between neophytes and archaeophytes is their residence times in invaded areas, which is much longer for archaeophytes than for neophytes (Pyšek *et al.*, 2004; Pyšek & Jarošík, 2005). For instance, neophytes are still being introduced and represent a continually expanding species pool with a much broader geographical origin (Pyšek *et al.*, 2003; Lambdon *et al.*, 2008). Because of their shorter residence time, many neophytes have probably not yet occupied all the suitable habitats. Therefore, Chytrý *et al.* (2008) hypothesize that the distribution of neophytes is relatively more dependent on propagule pressure and less dependent on habitat type than the distribution of archaeophytes.

From a more practical perspective, despite the weak correlation between frequency of aliens and their phylogenetic relatedness to native species, the main lesson learned for management activities against alien species is that it is unlikely that very 'unusual' species (i.e. species with very low phylogenetic relatedness to natives) will become highly successful invaders. In Fig. 1, all alien species with the highest NNPD values are quite unusual species without any congeneric relative in the native flora, such as *Anchusa arvensis* and *Echium vulgare* (Boraginaceae), *Hyoscyamus niger* (Solanaceae), *Sherardia arvensis* (Rubiaceae), *Verbena officinalis* (Verbenaceae),

Erodium cicutarium (Geraniaceae) or *Fumaria officinalis* (Papaveraceae) among archaeophytes, and *Parthenocissus inserta* (Vitaceae), *Elodea nuttallii* and *Elodea canadensis* (Hydrocharitaceae), *Pentaglottis sempervirens* and *Borago officinalis* (Boraginaceae), *Ailanthus altissima* (Simaroubaceae), *Sempervivum tectorum* (Crassulaceae), *Datura stramonium* and *Lycium barbarum* (Solanaceae), *Claytonia perfoliata* (Portulacaceae), *Syringa vulgaris* (Oleaceae) or *Asparagus officinalis* (Liliaceae) among neophytes.

The reasons why these species are unusual are varied: some of them originate from warmer regions (*Borago officinalis*, *Ailanthus altissima*, *Lycium barbarum*, *Syringa vulgaris*, *Pentaglottis sempervirens*). For these plants, it is therefore quite difficult to survive in the colder climate of Brussels. Some other species have particular soil requirements that render them unusual, such as calciphilous species (*Echium vulgare*, *Sherardia arvensis*), or species requiring a sandy soil texture (*Anchusa arvensis*, *Erodium cicutarium*, *Claytonia perfoliata*), both types of soil being rather uncommon in the city. Other species are simply barely used in Brussels plantations, and are therefore less frequent as spontaneous species (*Datura stramonium*, *Asparagus officinalis*). Finally, a number of species is also confined to uncommon habitats, i.e. old walls or roofs (*Sempervivum tectorum*, *Parthenocissus inserta*).

All these species belong to families that are generally rare both in the native and in the alien floras of Brussels; using simple randomization methods, we found that among the families totalling five or more species in at least one alien species group, archaeophytes in Brussels are significantly overrepresented in the family Brassicaceae, while neophytes are significantly overrepresented in the families Brassicaceae, Amaranthaceae and Geraniaceae, and significantly underrepresented by Poaceae. Also, the families Hydrocharitaceae, Portulacaceae, Simaroubaceae, Verbenaceae and Vitaceae are not present in the native flora of Brussels.

On the other hand, based on our data, the most dangerous alien species are those with high taxonomic similarity to natives and high propagule pressure; for Brussels, this means species such as *Coryza canadensis*, *Acer platanoides*, *Matricaria discoidea*, *Fallopia japonica*, *Robinia pseudoacacia* or *Galinsoga ciliata*. Phylogenetic relatedness between aliens and natives will help us foreseeing which species are more likely to invade where (Procheş *et al.*, 2008). This is particularly useful in situations where aliens are introduced (e.g. in private or public gardens, nurseries, horticultural industry) increasing the risk of biological invasions. Predicting a plant's invasiveness is indeed utmost important for conservation purposes, as invasive species have already altered a substantial part of the ecosystems on Earth. For instance, one could imagine that, next to other biological and environmental criteria, phylogenetic relatedness to natives can be used for compiling blacklists of alien species that would be prohibited for planting.

Nonetheless, as a general cautionary remark, it is worth emphasizing that applying a phylogenetic approach to studies aiming at predicting plant invasions, we encounter a major drawback: phylogenetic methods based on branch lengths can

be used only when the phylogenies are available for all plant species being studied. By contrast, so far available phylogenies usually contain pervasive polytomies below the family level that reduce their potential information content. Because of this lack of resolution, information on the phylogenetic distances between species is inevitably inaccurate. As better phylogenies of angiosperms become available, the reliability of the results obtained will increase accordingly.

Finally, although our analysis is limited to the city of Brussels, the observation that pre-adaptation to local environmental conditions represents an important constraint for the overall occupancy frequency of the most common aliens may be important even outside urban areas. Given the present-day climatic conditions of Central and Northern Europe, urban areas have been the main centres of immigration and establishment of alien species whose distribution is limited by the cooler temperatures of the surrounding areas (Deutschewitz *et al.*, 2003; Chytrý *et al.*, 2009). Nonetheless, under future climate-warming scenarios, successful urban aliens with a high pre-adaptation to warm and dry environmental conditions will most likely possess both the relevant functional characters and the dispersal potential to spread outside urban areas. Although this hypothesis may sound rather speculative, the importance of climatic conditions for the colonization of invaded regions by alien species has been demonstrated in a number of studies (e.g. Walther *et al.*, 2002; Thuiller *et al.*, 2004, 2005). Nobis *et al.* (2009) analysed the impact of climate change on the distribution of neophytes within the systematic national grid of the Swiss Biodiversity Monitoring program (456 square cells of 1 km²). They found that in contrast to native species, the prediction of neophyte richness at the landscape scale in Switzerland is mainly driven by temperature conditions. In the same vein, Michael Donoghue proposed the general principle that for plants 'it's easier to move than to evolve', meaning that under changing environmental conditions, 'it may be easier for species to migrate into an area with at least some of the relevant adaptations having already evolved, than it is for those adaptations to evolve in place' (Donoghue, 2008). As most Central and North European urban aliens possess higher temperature and aridity requirements with respect to the native flora of the surrounding natural and semi-natural areas, they seem an optimal species pool for testing this general principle under future global change scenarios.

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REFERENCES

- APG (2003) An update of the angiosperm phylogeny group classification for the orders and families of flowering plants: APG II. *Botanical Journal of the Linnean Society*, **141**, 399–436.
- Bose, A. & Chatterjee, S. (2003) Generalized bootstrap for estimators of minimizers of convex functions. *Journal of Statistical Planning and Inference*, **117**, 225–239.
- Cade, B.S. & Noon, B.R. (2003) A gentle introduction to quantile regression for ecologists. *Frontiers in Ecology and the Environment*, **1**, 412–420.
- Cade, B.S., Noon, B.R. & Flather, C.H. (2005) Quantile regression reveals hidden bias and uncertainty in habitat models. *Ecology*, **86**, 786–800.
- Chytrý, M., Pyšek, P., Tichý, L., Knollová, I. & Danihelka, J. (2005) Invasions by alien plants in the Czech Republic: a quantitative assessment across habitats. *Preslia*, **77**, 339–354.
- Chytrý, M., Maskell, L.C., Pino, J., Pyšek, P., Vilà, M., Font, X. & Smart, S.M. (2008) Habitat invasions by alien plants: a quantitative comparison among Mediterranean, subcontinental and oceanic regions of Europe. *Journal of Applied Ecology*, **45**, 448–458.
- Chytrý, M., Pyšek, P., Wild, J., Pino, J., Maskell, L.C. & Vilà, M. (2009) European map of alien plant invasions based on the quantitative assessment across habitats. *Diversity and Distributions*, **15**, 98–107.
- Daehler, C.C. (2001) Darwin's naturalization hypothesis revisited. *American Naturalist*, **158**, 324–330.
- Daehler, C.C. (2003) Performance comparisons of co-occurring native and alien plants: implications for conservation and restoration. *Annual Review of Ecology, Evolution and Systematics*, **34**, 183–211.
- Deutschewitz, K., Lausch, A., Kühn, I. & Klotz, S. (2003) Native and alien plant species richness in relation to spatial heterogeneity on a regional scale in Germany. *Global Ecology and Biogeography*, **12**, 299–311.
- Diez, J.M., Williams, P.A., Randall, R.P., Sullivan, J.J., Hulme, P.E. & Duncan, R.P. (2009) Learning from failures: testing broad taxonomic hypotheses about plant naturalization. *Ecology Letters*, **12**, 1174–1183.
- Donoghue, M.J. (2008) A phylogenetic perspective on the distribution of plant diversity. *Proceedings of the National Academy of Sciences USA*, **105**(Suppl. 1), 11549–11555.
- European Commission (2008) *Towards an EU strategy on invasive species*, COM(2008) 789. EC, Brussels.
- Gaston, K.J. (1994) *Rarity*. Chapman & Hall, London.
- Godefroid, S. (1996) Mise en évidence de la richesse floristique d'une grande ville: le cas de Bruxelles-Capitale. *Dumortiera*, **63**, 19–30.
- Godefroid, S. (2001) Analysis of the Brussels flora as indicator for changing environmental quality. *Landscape and Urban Planning*, **52**, 203–224.
- Godefroid, S. & Koedam, N. (2007) Urban plants species patterns are highly driven by density and function of built-up areas. *Landscape Ecology*, **22**, 1227–1239.
- Godefroid, S., Monbaliu, D. & Koedam, N. (2007) The role of soil and microclimatic variables in the distribution patterns of urban wasteland flora in Brussels, Belgium. *Landscape and Urban Planning*, **80**, 45–55.
- Gotelli, N. & Ellison, A. (2004) *A primer of ecological statistics*. Sinauer Associates, Sunderland, UK.
- IBGE (1999) *Atlas de la Flore de la Région de Bruxelles-Capitale*. Institut Bruxellois pour la Gestion de l'Environnement, Brussels.
- Knapp, S., Kühn, I., Schweiger, O. & Klotz, S. (2008a) Challenging urban species diversity: contrasting phylogenetic patterns across plant functional groups in Germany. *Ecology Letters*, **11**, 1054–1064.
- Knapp, S., Kühn, I., Wittig, R., Ozinga, W.A., Poschlod, P. & Klotz, S. (2008b) Urbanization causes shifts of species' trait state frequencies. *Preslia*, **80**, 375–388.
- Koenker, R.W. (1994) Confidence intervals for regression quantiles. *Asymptotic statistics* (ed. by P. Mandl and M. Huskova), pp. 349–359. Springer-Verlag, New York.
- Koenker, R. (2009) Quantreg: quantile regression. R package version 4.44. Available at: <http://www.r-project.org> (accessed 12 April 2010).
- Koenker, R. & Bassett, G. (1978) Regression quantiles. *Econometrica*, **46**, 33–50.
- Koenker, R. & Hallock, H. (2001) Quantile regression. *Journal of Economic Perspectives*, **15**, 143–156.
- Lambdon, P.W., Pyšek, P., Basnou, C. *et al.* (2008) Alien flora of Europe: species diversity, temporal trends, geographical patterns and research needs. *Preslia*, **80**, 101–149.
- LaSorte, F.A., McKinney, M.L., Pyšek, P., Klotz, S., Rapson, G.L., Celesti-Gradow, L. & Thompson, K. (2008) Distance decay of similarity among European urban floras: the impact of anthropogenic activities on beta diversity. *Global Ecology and Biogeography*, **17**, 363–371.
- Manly, B.F.J. (2007) *Randomization, bootstrap and Monte Carlo methods in biology*. Chapman and Hall/CRC, Boca Raton, FL.
- McDougall, A.S., Boucher, J., Turkington, R. & Bradfield, G.E. (2006) Patterns of plant invasion along an environmental stress gradient. *Journal of Vegetation Science*, **17**, 47–56.
- McKinney, M.L. (2006) Urbanization as a major cause of biotic homogenization. *Biological Conservation*, **127**, 247–260.
- Muth, N.Z. & Pigliucci, M. (2007) Implementation of a novel framework for assessing species plasticity in biological invasions: responses of *Centaurea* and *Crepis* to phosphorus and water availability. *Journal of Ecology*, **95**, 1001–1013.
- Nobis, M.P., Jaeger, J.A.G. & Zimmermann, N.E. (2009) Neophyte species richness at the landscape scale under urban sprawl and climate warming. *Diversity and Distributions*, **15**, 928–939.
- Procheş, S., Wilson, J.R.U., Richardson, D.M. & Rejmánek, M. (2008) Searching for phylogenetic pattern in biological invasions. *Global Ecology and Biogeography*, **17**, 5–10.
- Pyšek, P. (1995) On the terminology used in plant invasion studies. *Plant invasions – general aspects and special problems* (ed. by P. Pyšek, K. Prach, M. Rejmánek and M. Wade), pp. 71–81. SPB Academic Publishers, Amsterdam.

- Pyšek, P. (1998) Alien and native species in central European urban floras: a quantitative comparison. *Journal of Biogeography*, **25**, 155–163.
- Pyšek, P. & Jarošík, V. (2005) Residence time determines the distribution of alien plants. *Invasive plants: ecological and agricultural aspects* (ed. by Inderjit), pp. 77–96. Birkhäuser Verlag, Basel, CH.
- Pyšek, P. & Richardson, D.M. (2007) Traits associated with invasiveness in alien plants: where do we stand?. *Biological invasions* (ed. by W. Nentwig), pp. 97–126. Springer Verlag, Berlin.
- Pyšek, P., Sádlo, J. & Mandák, B. (2002) Catalogue of alien plants of the Czech Republic. *Preslia*, **74**, 97–186.
- Pyšek, P., Jarošík, V. & Kučera, T. (2003) Inclusion of native and alien species in temperate nature reserves: an historical study from Central Europe. *Conservation Biology*, **17**, 1414–1424.
- Pyšek, P., Richardson, D.M., Rejmánek, M., Webster, G., Williamson, M. & Kirschner, J. (2004) Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. *Taxon*, **53**, 131–143.
- Pyšek, P., Jarošík, V., Chytrý, M., Kropáč, Z., Tichý, L. & Wild, J. (2005) Alien plants in temperate weed communities: prehistoric and recent invaders occupy different habitats. *Ecology*, **86**, 772–785.
- Rejmánek, M. (1996) A theory of seed plant invasiveness: the first sketch. *Biological Conservation*, **78**, 171–181.
- Ricotta, C., Godefroid, S. & Celesti-Grapow, L. (2008) Common species have lower taxonomic diversity: evidence from the urban floras of Brussels and Rome. *Diversity and Distributions*, **14**, 530–537.
- Ricotta, C., LaSorte, F.A., Pyšek, P., Rapson, G.L., Celesti-Grapow, L. & Thompson, K. (2009) Phyloecology of urban alien floras. *Journal of Ecology*, **97**, 1243–1251.
- Rocchini, D. & Cade, B.S. (2008) Quantile regression applied to spectral distance decay. *IEEE Geoscience and Remote Sensing Letters*, **5**, 640–643.
- Strauss, S.Y., Webb, C.O. & Salamin, N. (2006) Exotic taxa less related to native species are more invasive. *Proceedings of the National Academy of Sciences USA*, **103**, 5841–5845.
- Sukopp, H. (2004) Human-caused impact on preserved vegetation. *Landscape and Urban Planning*, **68**, 347–355.
- Sukopp, H. & Werner, P. (1983) Urban environments and vegetation. *Man's impact on vegetation* (ed. by W. Holzner, M.J.A. Werger and I. Ikusima), pp. 247–260. Dr. W. Junk Academic Publisher, The Hague.
- Swenson, N.G., Enquist, B.J., Thompson, J. & Zimmerman, J.K. (2007) The influence of spatial and size scale on phylogenetic relatedness in tropical forest communities. *Ecology*, **88**, 1770–1780.
- Thompson, K. & McCarthy, M.A. (2008) Traits of British alien and native urban plants. *Journal of Ecology*, **96**, 853–859.
- Thompson, K., Hodgson, J.G. & Rich, T.C.G. (1995) Native and alien invasive plants: more of the same? *Ecography*, **18**, 390–402.
- Thuiller, W., Araújo, M.B. & Lavorel, S. (2004) Do we need land-cover data to model species distributions in Europe? *Journal of Biogeography*, **31**, 353–361.
- Thuiller, W., Richardson, D.M., Pyšek, P., Midgley, G.F., Hughes, G.O. & Rouget, M. (2005) Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. *Global Change Biology*, **11**, 2234–2250.
- Vamosi, S.M., Heard, S.B., Vamosi, J.C. & Webb, C.O. (2009) Emerging patterns in the comparative analysis of phylogenetic community structure. *Molecular Ecology*, **18**, 572–592.
- Vilà, M. & Weiner, J. (2004) Are invasive plant species better competitors than native plant species? Evidence from pairwise experiments. *Oikos*, **105**, 229–238.
- Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guldberg, O. & Bairlein, F. (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.
- Webb, C.O. (2000) Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. *American Naturalist*, **156**, 145–155.
- Webb, C.O. & Donoghue, M.J. (2005) Phylomatic: tree assembly for applied phylogenetics. *Molecular Ecology Notes*, **5**, 181–183.
- Webb, C.O., Ackerly, D.D., McPeck, M.A. & Donoghue, M.J. (2002) Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, **33**, 475–505.
- Wikstrom, N., Savolainen, V. & Chase, M.W. (2001) Evolution of angiosperms: calibrating the family tree. *Proceedings of the Royal Society, Series B*, **268**, 2211–2220.
- Williamson, M. & Gaston, K.J. (1999) A simple transformation for sets of range sizes. *Ecography*, **22**, 674–680.
- Wittig, R. (2004) The origin and development of the urban flora of Central Europe. *Urban Ecosystems*, **7**, 323–333.

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