



Do railway edges provide functional connectivity for plant communities in an urban context?

Caterina Penone*, Nathalie Machon, Romain Julliard, Isabelle Le Viol

Muséum National d'Histoire Naturelle CERSP UMR 7204 MNHN-CNRS-UPMC, 55 rue Buffon, 75005 Paris, France

ARTICLE INFO

Article history:

Received 17 September 2011

Received in revised form 10 January 2012

Accepted 16 January 2012

Available online 11 February 2012

Keywords:

Dispersal

Mobility

Plant traits

Structural connectivity

Transport network

ABSTRACT

Functional connectivity is essential to maintaining biodiversity in fragmented landscapes but little attention has been given to structures that can provide it in an urban context. Using both the taxonomic and functional diversity of semi-natural grassland plant communities, we assessed the functional connectivity of linear transportation infrastructures in urban landscape. We sampled the vegetation at 71 study sites located along the edges of two railway lines. We hypothesised that if railways favour functional connectivity, then spatially connected communities should be more similar than disconnected communities. Therefore, we compared floristic dissimilarities between site pairs that were either connected or separated by a railway spatial break (overpass or station). As a further approach, we supposed that functional connectivity may attenuate the effect of urbanisation filters on plant communities. Thus we examined whether and how edges' plant communities were influenced by urbanisation and compared our results to the patterns described in the literature. Functional connectivity was mainly maintained at railway stations, contrary to overpasses, which seemed to interrupt dispersal, demonstrating that railway edges provide connectivity for some but not all functional groups: this was only true for moderately mobile species. Surprisingly, railway edges did not seem to play an additional connective function for invasive species, the presence of which being strongly related to the urbanisation intensity and not influenced by spatial breaks along railways. Our study thus highlights the potential function of railway edges as corridors for common grassland plants. Landscape managers should include railways in green networks to improve connectivity in urban landscapes.

© 2012 Elsevier Ltd. All rights reserved.

1. Introduction

Habitat fragmentation is considered a severe local, regional and global perturbation that affects biotic communities (Debinski and Holt, 2000; Fahrig, 2003). Fragmented landscapes are characterised by small patches that are isolated from each other by a matrix that acts as a selective filter for species movement (Lawton, 1999; Wilcove et al., 1986). In such landscapes, connectivity is considered a key issue for biodiversity conservation (Taylor et al., 1993; Wehling and Diekmann, 2009). Therefore, it is of great importance to identify connectivity and the spatial arrangements of habitat patches providing it (i.e. corridors or stepping stones) to assist with the decisions of conservation practitioners regarding landscape management. Through habitat loss and isolation, fragmentation affects community richness, composition and species interactions (Fahrig, 2003). A species' vulnerability to fragmentation varies among functional species traits: dispersal abilities and species mobility are considered key traits for explaining species responses

to fragmentation (see review by Ewers and Didham (2006) and Schleicher et al. (2011)), and they can be used to identify connectivity in linear habitat patches. As illustrated by Doerr et al. (2011), structural connectivity is a component of functional connectivity; an interruption of the first should result in an interruption of the second, thus having an effect on less mobile species. In our study, we used this assumption as an indirect method to test functional connectivity in linear patches.

In habitat patches, plant composition is determined by biotic and abiotic filters (Knapp et al., 2008a; Zobel, 1997) that select species with suitable functional traits from a species pool through dispersal and survival (Roy and de Blois, 2006; Williams et al., 2009). The effects of these filters on taxonomic and functional communities are particularly strong in urban landscapes, where small and isolated patches of habitat (e.g. private or public gardens) are situated within a human dominated matrix (Stenhouse, 2004). Urban filters are, in part, linked to environmental conditions such as higher temperatures or higher nitrogen levels due to pollution (McDonnell et al., 1997; Pellissier et al., 2008) (hereafter environmental urbanisation effects). Human preferences also act as filters causing species gain (mainly of exotic species) and losses

* Corresponding author. Tel.: +33 140 798 114; fax: +33 140 793 835.

E-mail address: penone@mnhn.fr (C. Penone).

(Williams et al., 2009). Other urban filters, such as habitat size or dispersal barriers, are due to fragmentation and isolation (Grimm et al., 2008) (structural urbanisation effects), and their effects on biotic communities should be attenuated by connectivity (Tewksbury et al., 2002). If linear patches provide structural connectivity, an attenuation of these urbanisation effects on taxonomic and functional plant communities should be observed when compared with the urbanisation effects described in the literature. We used this assumption as a supplementary approach to assess functional connectivity in railway edges. Although urban landscapes are strongly fragmented (Stenhouse, 2004), connectivity has been poorly studied in this context (but see Kowarik and von der Lippe, 2011; Schleicher et al., 2011). Transportation networks are mainly considered to be barriers for connectivity (Jackson and Fahrig, 2011) or corridors for invasive species (Brown et al., 2006). However, in urban landscapes, railways ensure structural connectivity (Calabrese and Fagan, 2004) because their vegetated edges penetrate into dense urban areas, similarly to rivers or to some roads. Despite their potential for connectivity in an anthropogenic context, their functional connectivity has been poorly studied (but see Tikka et al., 2001), and most studies focus on invasive species (Hansen and Cleverger, 2005).

In the present study, we analyse the potential connectivity of railway edges for plant communities in an urban context. We hypothesise that if railway edges favour connectivity, spatially connected communities within railway edges should be more similar than disconnected communities. Railway structural connectivity is regularly interrupted by spatial breaks, such as overpasses and stations. We therefore assumed that although railway edges provide functional connectivity, they can be disrupted by railway breaks. We tested this assumption by comparing floristic dissimilarities between sites located along railway edges that were either connected or separated by a railway break, this comparison was done for different functional species traits. As a supplementary approach, in order to discuss the results that we obtained, we hypothesised that if railway edges favour connectivity this should attenuate the effect of urbanisation filters (those due to fragmentation and isolation) on plant communities. We thus examined the effect of urbanisation intensity on species richness, diversity and trait composition, and we compared our results with the patterns described in literature.

2. Materials and methods

2.1. Study sites and data collection

The study was conducted along two long-established railway lines (built in 1840 and 1847) in the south of the Parisian region, France (Fig. 1). This region is densely populated, with 20% of the national population living in just 2% of the nation's land area. The two lines traverse a landscape structured by different degrees of urbanisation, as they cross numerous cities and towns from the south of the region towards the centre of Paris. The vegetation found along the borders of the train tracks is mainly spontaneous as the edges have not been planted or sown since their construction and is principally interrupted by railway stations and overpasses. The study sites were all mown approximately at the same time during the summer, 2 years before the study (SNCF, French National Railways, personal communication).

As we wanted to test the effect of railway continuity and landscape urbanisation on railway plant communities, sites were chosen to minimise variations in other environmental variables and to be isolated from other habitat patches. Thus, we tried to standardise sites using aerial photographs and field surveys. All sites were selected with the following two characteristics: (1) they were

bordered by the same environment: on one side ballast (crushed rock) and rails, and on the other side a small paved road (or a parking lot) and dwellings; (2) they exhibited the same features: grassland vegetation less than 1 m in height and similar border width and slope (Fig. 1). Note that ballast was treated twice a year with a non-selective herbicide for safety reasons, therefore there were almost no plants growing in ballast. This practice cannot be changed at the moment because there are not economic alternative solutions (SNCF, personal communication). Based on these criteria, we identified 71 study sites along the two lines (n1 and n2, respectively) located between 70 and 4 km from the centre of Paris. Each site consisted of a 4- to 8-m-wide (6 ± 1.4 s.d.) grassy embankment that was at least 50 m from the nearest large tree. The distance between two consecutive sites varied between 0.2 and 25 km, with an average distance of 3.3 km. Within the centre of each site, we established a 50 m-long transect 4 m from the rails, and we inventoried all vascular plants in five sample quadrates (1 m^2) distributed every 10 m. All taxa, except *Taraxacum*, were identified to the species level according to the French Flora Index (Kerguelen, 2003) and the International Plant Names Index (IPNI, 2008). In order to check for potential soil differences between sites, we measured soil pH, texture, colour, compaction, and stoniness.

2.2. Spatial breaks and urbanisation measure

Using the French railway company database (personal communication), aerial photographs and field observations, we identified and located the two main kinds of spatial breaks in vegetation connectivity: railway stations and overpasses (main length $12.2 \text{ m} \pm 21$ s.d.). To take into account the effects of urbanisation on plant communities, we defined a circular 200 m-wide buffer (which radius has been shown to be appropriate for flora studies (Muratet et al., 2007)) around each site using GIS (ARCGIS 9.3/ESRI). Then we determined the areas of the main land cover types (woodland, farmland, urban) in the surrounding landscape of each site using a detailed, regional geo-referenced land use database of landscape features (IAURIF, 2003). Urban cover was defined as the proportion of built and paved surfaces and it varied between 26.8% and 82.5% (55.3 ± 18.3 s.d.), with the lowest values corresponding to higher proportions of woodland (mean 19.5 ± 18.7); farmland habitat was scarce along our study lines (mean 1.0 ± 2.9 s.d.). Note that our study sites were located in more or less densely urbanised areas but not in a complete gradient (i.e. varying from 0% to 100%) because sites were chosen with the aim to minimise the variation of environmental covariables. Indeed, at a finer scale, within a 50 m-wide buffer, urban cover was high and similar across sites (mean $89\% \pm 15$ s.d.), which confirmed that we chose sites with a similar configuration.

2.3. Species functional traits and species mobility

To assess the influence of railway spatial breaks on community functional composition, species were characterised by their functional traits. Data were mainly taken from the Bioflor database (Klotz et al., 2002), LEDA traitbase (Kleyer et al., 2008) and from literature reviews (Appendix A). Some traits were grouped to minimise bias due to rare classes: myrmecochory was included in epizoochory, and autochory and barochory were merged. Chi-square tests among traits were computed to select uncorrelated traits. We retained floristic status (exotic), invasiveness (subgroup of exotic), and dispersal traits as follows: pollen vector (wind, insect, selfing); reproduction (seed, mixed seed and vegetative); and dispersal mode (anemochory, barochory, zoochory (endozoochory, epizoochory)).

As connectivity is also related to species mobility (Ewers and Didham, 2006; Matlack and Monde, 2004; Ockinger et al., 2010),

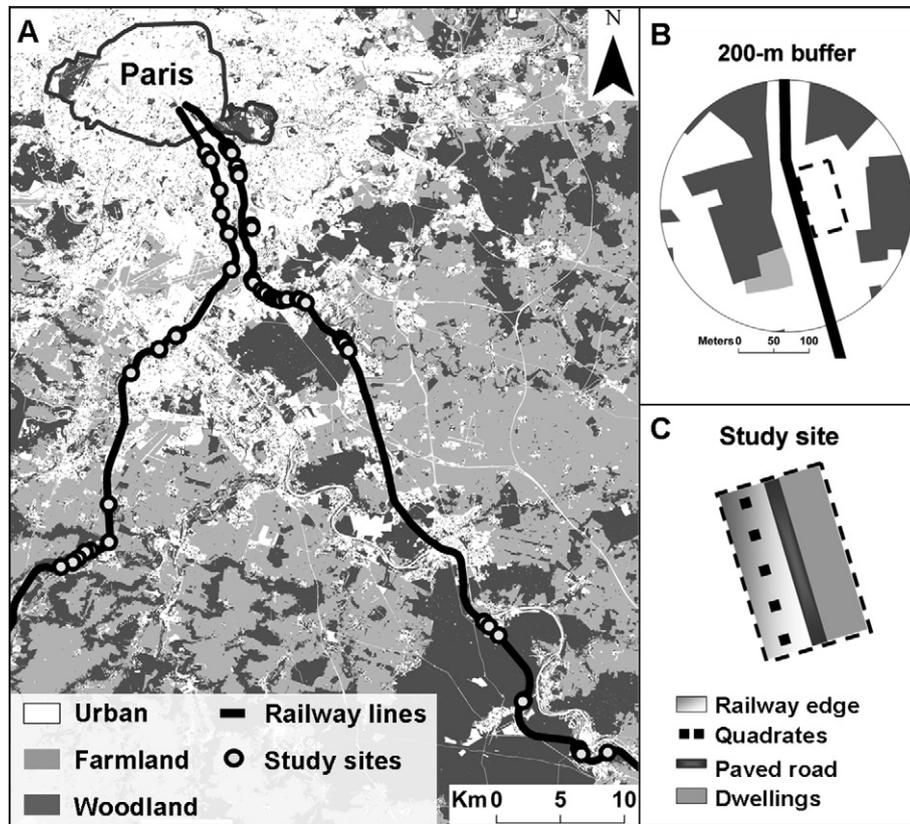


Fig. 1. Map of site locations and configuration of study sites. Each study site was bordered by the same environment: on one side ballast and rails and on the other side, a small paved road and dwellings (C). We built 200-m buffers (B) around the 71 sites (A) and determined the areas of the main land cover types. Vascular plants were inventoried in five sample quadrats (1 m²) distributed every 10 m (C).

we categorised dispersal traits into three degrees of “mobility” according to literature-defined dispersal distances associated with these traits: (1) wind pollination was a highly mobile species trait (Okubo and Levin, 1989); (2) insect pollination (Pasquet et al., 2008), anemochory (Vittoz and Engler, 2007) and zoochory (Gomez and Espadaler, 1998) were moderately mobile; and (3) self-pollination and barochory were poorly mobile. The mobility difference between anemochory and wind pollination is mainly due to the weight of propagules, that is, seeds heavier than pollen (Vittoz and Engler, 2007). Although it is difficult to categorise reproductive traits according to their mobility, in general, species with seed reproduction may disperse over larger distances than species with vegetative reproduction only (Winkler and Fischer, 2001). Note that pollination mode does not give information about where a plant species moves to but it helps to determine whether plants can persist in a site (Mayfield et al., 2006).

To assess urban abiotic environmental filtering on plant traits, Ellenberg indicator values were assigned to each species (Ellenberg et al., 1992). These values rank the flora on a relative 9° scale (12 for moisture); they reflect species preferences and in particular their affinity or tolerance to light, temperature, soil moisture, soil acidity and nitrogen soil level. We distinguished two kinds of species traits: (1) those that should respond to urban environmental effects (e.g. Ellenberg traits) and (2) those that should respond to structural urbanisation effects (e.g. dispersal traits).

2.4. Data analyses

2.4.1. Railway spatial break effects on plant communities

We examined whether the disruption of spatial structural connectivity resulted in a higher difference in community composi-

tion. Taking into account spatial autocorrelation, the distribution of habitats in the surrounding landscape and the presence of stations or overpasses, we firstly assessed if floristic dissimilarities were greater between sites located on two different railway lines than between sites located on the same railway line (hereafter “railway_line”). Secondly we examined whether spatial breaks in the form of stations and overpasses resulted in greater floristic dissimilarities between interrupted sites than between non-interrupted sites within a railway line (hereafter “break_type”). To account for taxonomic and functional composition, tests were performed for all species and plant trait subsets, i.e., groups of species exhibiting the same trait value. The matrices of floristic dissimilarities between sites were calculated based on species frequency using the Bray–Curtis index for both railway lines. This measure includes relative abundance information and excludes joint absences (Anderson et al., 2011). Note also that Bray–Curtis index is adapted when sampling effort is equivalent among communities, which is the case in our study. Species were first separated according to functional traits, then Bray–Curtis index was calculated for each subset of species. For the “railway_line” analysis we built connectivity break matrices including every pair of sites and using three values: 0 (non-interrupted sites), 1 (sites interrupted by an overpass or a station) and 2 (sites on different railway lines). For the analysis on railway spatial breaks (“break_type”) the analyses were performed for the two lines separately using a matrix with either a 0 (non-interrupted) or a 1 (interrupted) depending on whether or not there was a break between them. Given the spatial structure of our sampling design, we took into account spatial autocorrelation by adding geographic distance matrices to our models. Indeed, it could be expected that site pairs located closely together have more similar floristic compositions than distantly

related site pairs. The effect of breaks on floristic dissimilarities between sites was tested using partial Mantel tests (999 random permutation tests, package *ecodist* in R) with the connectivity break matrix as predictor variable and with the following matrices as covariables: (1) geographic distance (Euclidean distance); (2) urbanisation dissimilarity, calculated using the Bray–Curtis dissimilarity index on the percent of urbanisation per site; and (3) site position, which indicated whether the sites were at the same side of the railway (0) or not (1). The analyses were firstly performed including all the sites (“*railway_line* analysis”) and secondly for the two railway lines separately (“*break_type* analysis”). For the latter, the effect of station and overpass was tested together and separately.

In addition, we tested whether the presence of railway breaks resulted in greater urbanisation dissimilarities between sites using Mantel tests. Furthermore, as the site adjacent surface varied (road or parking lots) and since roads and parking lots may have different impacts on biological fluxes, we checked for the absence of correlations between the type of adjacent surface and species richness and diversity using the F-test.

2.4.2. Urbanisation effects on species richness, diversity and traits

We first assessed the effect of urbanisation intensity on species richness and diversity at the quadrat scale using Generalised Estimating Equations (GEEs, package *geepack* in R) and at the site scale (i.e., cumulative richness over five quadrats) using generalised linear models (GLMs). We used a Gaussian distribution for diversity and a Poisson distribution for richness (hereafter urbanisation analysis). Species diversity was calculated using both the Shannon and Simpson indices. For the functional analysis, we examined at site scale the effect of urbanisation intensity on trait composition by examining the relationship between species frequencies (i.e., the proportion of quadrats where the species were found) and species traits using generalised linear models with a binomial family and logit link. The urbanisation by trait interaction (predictor variable) was used to examine whether species frequency (response variable) varied with urbanisation intensity as a function of the trait value. As average species frequency does vary among plant species and among sites, we included into the model the species and the site in order to account for variance explained by those factors. The effect of urbanisation intensity on species traits (urbanisation by trait interaction) was tested accounting for the effect of urbanisation on species (urbanisation by species interaction). Firstly, analyses were run separately for each trait and secondly all traits found significant were tested in the same model. Since invasive was a subset of exotic, two separate models were run for these traits. All analyses were conducted with R version 2.10.1 (R Development Core Team, 2009).

3. Results

In 71 sites, we observed a total of 186 plant species (Appendix B). Within a 5 m² site, the species richness ranged from 6 to 32 (18.9 ± 5.9 s.d.). Most of these species were not restricted to the railway edges, indeed 95% ($n = 177$) of them were also recorded in a large study on urban flora conducted in the Parisian region by Muratet et al. (2008).

Taking into account spatial autocorrelation, the distribution of habitats in the surrounding landscape and the presence of stations or overpasses, floristic distances were greater between sites located on two different railway lines than sites located within the same line (see Table 1) except for wind pollinated, endozoochory and invasive species. Floristic dissimilarities between sites were significantly higher in presence of overpasses while stations had weak effects (see Table 1). Mantel tests on dispersal traits showed that all floristic dissimilarities, except for wind pollinated species

and endozoochory, were significantly higher in the presence of breaks (Table 1). However, results differed between the two lines for the invasive species group, the epizoochory group and the self-pollinating species group. Railway overpasses were related to a higher floristic dissimilarity for the following traits: insect pollination, anemochory, exotic species, seed and mixed reproduction. In contrast, presence of overpasses did not result in greater floristic dissimilarities for invasive species, endozoochory and wind pollination. For other traits, the two railway lines gave contrasting results. The presence of stations was not related to a higher floristic dissimilarity between sites, except for the mixed reproduction and the insect-pollinating (only for one railway line) groups. Note that the presence of railway breaks was not related to urbanisation intensity. Further information on the effect of covariables is given in Table C.1 (Appendix C).

No significant relationship was found between urbanisation (urbanisation analysis) and total species richness, the Shannon and Simpson diversity or dispersal traits at both the quadrat (richness $P = 0.59$, Shannon $P = 0.64$, Simpson $P = 0.81$) and site scales (richness $P = 0.11$, Shannon $P = 0.27$, Simpson $P = 0.34$). We found a positive correlation between urbanisation and the frequencies of invasive and exotic species as well as for species exhibiting affinity for high temperatures and nitrogen soil levels (Table 2). The correlations with urbanisation were negative for high moisture tolerant species. Note that the type of adjacent surface (road or parking lot) had no significant effect on plant community richness ($P = 0.18$) or diversity (Shannon $P = 0.25$; Simpson $P = 0.26$). In addition, we did not find any significant relationship between urbanisation intensity, distance to Paris and soil parameters.

4. Discussion

Our study on railway breaks suggested that railway edges provide functional connectivity. Indeed, the railway breaks had an effect on most species and dispersal traits, which is consistent with our hypothesis: spatially connected communities were more similar than disconnected communities. Railway stations, in contrast to overpasses, did not affected functional connectivity for most of the studied traits. It is unlikely that this difference was due to our study design or to a lack of statistical power, as we conducted the same tests and used presence–absence data in the analyses of both stations and overpasses.

Furthermore, the lack of urbanisation intensity effects on plant richness and diversity could mean that railway edges provide functional connectivity. Indeed, connectivity is likely to attenuate those effects of urbanisation that are linked to fragmentation and isolation (structural effects) because it is supposed to improve the link between communities. Actually, most studies on the effect of urbanisation on plant communities conducted at many different spatial scales have found that plant richness increases with moderate urbanisation (i.e. having 20–50% impervious surface area) but decreases with low or high urbanisation (i.e. less than 20% or over 50% impervious surfaces) (see review by McKinney (2008)). Moreover urbanisation has also been shown to affect plant diversity either positively or negatively depending on the presence of exotic species (Burton et al., 2005; Pennington et al., 2010). But note also that, due to site standardisation, in our sampling design low levels (<20%) of urbanisation were not represented, therefore we could only detect changes in richness at moderate or high urbanisation levels. It should also be noticed that if urbanisation effects appear at finer scales than 200 m (e.g. 50 m) we were not able to detect them. Indeed, at small scale our sites had a similar and high urban cover as they were always bordered by a road and dwellings.

At the same time, our results on nitrophilous species (Ellenberg nutrient affinity) were similar to those found in literature (Knapp

Table 1
Railway break effects on plant traits. Results of partial Mantel test for the two railway lines tested together and separately (n1 and n2) are given.

Predictor variable	Railway line		All breaks				Overpasses				Stations				
	Both		n1	n2			n1	n2			n1	n2			
Railway line	71		45	27			45	27			45	27			
Number of sites															
	<i>N</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>
All species	187	0.001	0.08	0.001	0.2	0.001	0.25	0.001	0.16	0.001	0.24	0.05	0.10	0.05	0.12
Exotic	33	0.004	0.05	0.001	0.2	0.001	0.25	0.001	0.16	0.001	0.24	0.33	0.02	0.23	0.04
Invasive	10	0.07	0.02	0.02	0.1	0.08	0.09	0.13	0.04	0.05	0.09	0.73	−0.02	0.41	0.006
<i>Reproductive mode</i>															
Seed	106	0.001	0.07	0.001	0.2	0.002	0.21	0.007	0.12	0.004	0.20	0.13	0.06	0.13	0.08
Mixed	80	0.003	0.05	0.001	0.2	0.001	0.22	0.004	0.16	0.001	0.23	0.23	0.04	0.08	0.10
<i>Dispersal mode</i>															
Anemochory	58	0.001	0.10	0.001	0.2	0.007	0.16	0.001	0.18	0.006	0.16	0.07	0.09	0.08	0.08
Barochory	57	0.007	0.05	0.002	0.1	0.001	0.20	0.06	0.10	0.003	0.23	0.07	0.08	0.11	0.09
Zoochory	68	0.001	0.07	0.01	0.1	0.01	0.16	0.11	0.07	0.01	0.17	0.32	0.03	0.36	0.03
Endozoochory	13	0.310	0.009	0.71	−0.02	0.32	0.02	0.81	−0.04	0.32	0.02	0.13	0.06	0.09	0.09
Epizoochory	55	0.003	0.07	0.06	0.06	0.02	0.16	0.19	0.05	0.007	0.16	0.41	0.01	0.37	0.02
<i>Pollen vector</i>															
Wind	34	0.416	0.005	0.06	0.06	0.16	0.07	0.12	0.07	0.17	0.07	0.51	−0.003	0.44	0.005
Insect	110	0.001	0.09	0.001	0.2	0.001	0.24	0.002	0.15	0.001	0.24	0.03	0.11	0.11	0.08
Selfing	41	0.022	0.04	0.01	0.1	0.06	0.09	0.03	0.08	0.06	0.09	0.002	0.15	0.01	0.16

N is the number of species used to calculate the Bray–Curtis dissimilarity indexes between sites.
r: Mantel coefficient – *P*: one-tailed *p*-value (null hypothesis: $r \leq 0$) – significant results are in bold.

Table 2
The effects of urbanisation on plant traits.

Plant traits	<i>N</i> ^a	Effect direction	<i>P</i>
Floristic status^b			0.021
Exotic	33	+	
Indigenous	153	−	
Invasiveness^b			0.009
Invasive	10	+	
Non-invasive	176	−	
Reproductive mode^b			0.350
Seed reproduction	106	+	
Mixed reproduction	80	−	
Dispersal mode^b			0.616
Anemochory	58	−	
Barochory	57	−	
Zoochory	68	+	
Pollen vector^b			0.931
Wind pollination	34	−	
Insect pollination	110	+	
Selfing pollination	41	+	
Light affinity(ellL) ^c	170	−	0.882
Temperature affinity(ellT) ^c	136	+	0.006
Soil moisture affinity(ellM) ^c	150	−	<0.001
Soil acidity affinity(ellK) ^c	142	−	0.983
Nitrogen soil level affinity(ellN) ^c	151	+	<0.001

P-values from the ANOVA associated with the calculated *F*-ratio distribution function are given. Since invasive was a subset of exotic, two separate models were run for these traits.

All traits found significant were tested in the same model. Here is an example of the model for invasive (or exotic) species: species_frequency ~ site + species + urb:ellF + urb:ellT + urb:ellN + urb:reproduction + urb:invasive (or exotic) + urb:species.

^a *N* is the number of species for which trait information was available.

^b Categorical traits: one *P*-value is given for each group of traits.

^c Numerical traits: one *P*-value is given for each trait.

et al., 2008b; Lososová et al., 2006; Pellissier et al., 2008; Vallet et al., 2010). Furthermore we found that plants with affinity for high temperatures were more frequent in urban environments that are generally characterised by higher temperatures than suburban zones (heat island effect Grimm et al., 2008). These results highlighted that some environmental urbanisation effects were detectable with our sampling design. These effects cannot be counteracted by

connectivity because they are linked to environmental conditions like soil properties or temperature.

However, the functional connectivity of the railways differed according to the species' dispersal capabilities.

4.1. Highly and poorly mobile species

We found that highly mobile species traits were not affected by edge breaks and that there were not significant differences between railway lines concerning wind pollinated species. Highly mobile species might be able to overcome railway breaks as their dispersal distances can be quite large (e.g. 1 km, Hoyle and Cresswell, 2009) and they may also be able to disperse from other habitat patches to the railways. Even if wind pollinated species are highly mobile, some authors found that they are affected by urbanisation either positively or negatively (Douda, 2010; Knapp et al., 2008b; Lososová et al., 2006), but in this study we did not find any urbanisation effect on this trait. Assuming that our sampling design could detect an urbanisation effect on this species trait, and hypothesising that connectivity should attenuate the effects of urbanisation, this may highlight a connectivity effect of railway edges for highly mobile species. In urban context wind conditions depend on buildings structure and railway lines can be corridors of wind because no barrier stops it. This passage-effect probably benefits to wind-pollinated species and could explain the difference between our results and the results of other studies.

For poorly mobile species, the two railway lines gave contrasting results in the spatial break analysis; however we found an effect of geographic distance on these species that may result from a connectivity effect of railway edges. Since their dispersal is mainly linked to strictly local factors, such as the surrounding slope in the case of barochory (Morimoto et al., 2010), the connectivity function may have to be considered along larger time scales than for other species traits.

4.2. Moderately mobile species

For moderately mobile species, functional connectivity seemed to be ensured in continuous railway sections (between two breaks) because we found a railway break effect on these species. However,

these sections are sometimes quite long (e.g., more than 5 km in our study). Many authors have shown that trains and cars can contribute to seed dispersal, including long-distance dispersal events (Von der Lippe and Kowarik, 2007). The slipstream of trains, which likely carry anemochorous seeds, can be interrupted by air turbulence or crosswind (Barcala and Meseguer, 2007) when the train traverses overpasses (as shown by Ernst (1998) for achenes). This air flow may also be interrupted when trains slow down or stop at stations. In stations, seeds may then be picked up again by air turbulence or wind. In contrast, seeds likely fall from overpasses, as these have very narrow paved edges, which may explain the difference between stations and overpasses.

Animal mobility can explain the different responses to breaks we found for insect-pollinated, epizoochorous and endozoochorous species. Vittoz and Engler (2007) found that endozoochorous species have moderately or highly mobile seeds, as they are mainly transported by birds or large vertebrates. The lack of railway break effects on endozoochorous species may reflect the fact that vertebrates move along edges or cross the railway often. Concerning birds, even if their movement is influenced by anthropogenic linear features (forest songbirds for example), they can easily fly over bridges (Tremblay and St. Clair, 2009). Thus, these structures are not spatial breaks for birds. In contrast, epizoochorous seeds are carried by terrestrial animals (Vittoz and Engler, 2007) that may be disturbed by paved surfaces and the presence of humans (stations). Similarly, insects that ensure pollination are likely influenced by railway breaks. For example, a break in vegetation continuity, even if minor, has been demonstrated to have an effect on bee movement such that bees make more flights within a patch than between two patches (Pasquet et al., 2008). This may also explain the effect of the presence of stations on insect pollinated plants.

Interestingly, our results on the effect of spatial breaks on plant traits are similar to the results of Thomas (2000) on fragmentation effects on butterflies. Thomas' study showed that butterflies with intermediate mobility are more sensitive to fragmentation than either highly or poorly mobile butterflies. These results highlight the importance of considering functional connectivity through species traits and, in particular, species mobility. Even if more research is required, and other fragmentation indicators are surely necessary, species mobility may be a valuable tool for comparing functional connectivity between habitat patches for many species; however, it requires good knowledge of species traits.

4.3. Invasive and exotic species

There was no evidence that invasive species community similarities were affected by overpasses. The well-known urbanisation effect on invasive species (i.e. increased species number or frequencies of invasive species in urban areas) was detected across our study sites and not attenuated by the expected connectivity provided by railways. Hence, railway edges did not seem to play an additional connective function for invasive species. This issue is inconsistent with many studies on other transport networks (roadsides, highways), which demonstrated their function as corridors for invasive species (Ernst, 1998; Hansen and Clevenger, 2005). However our results have to be considered with caution because they are based on only ten species. Nevertheless, the urbanisation effect on exotic and invasive species was similar at the railway edges and in other urbanisation studies. Indeed, we found 22 studies that analysed the impact of urbanisation on exotic and invasive species, all of them (except one) found a positive effect of urbanisation on invasive or exotic plants (see details in Appendix D). The higher frequency of exotic and invasive species in urban landscapes seems to largely result from the presence of sources rather than from fragmentation (or the lack of functional corridors in the urban

matrix), as urban areas are prone to exotic and invasive plant introductions (McKinney, 2004; Pyšek, 1998). Furthermore, invasive species often grow in disturbed communities, which are common in urban contexts (Marzluff et al., 2008). Environmental filters such as temperature, moisture and nutrients may also partially explain higher frequencies of invasive and exotic species in urbanised landscapes (Knapp et al., 2009), which may reflect their origins in warmer and dryer areas.

We cannot conclude about a corridor function of railway edges, however even if railways might be corridors for exotic species, the frequency of invasive and exotic species seems to be much more related to the urban context (presence of sources, higher levels of disturbance, abiotic conditions) than to the connectivity of railway edges. An alternative hypothesis is that the distribution of exotic (and invasive) species is not at equilibrium and that railway connectivity did not have time to homogenise the source effect from the urban area (Botham et al., 2009).

5. Conclusions and implications for management and conservation

Through a study of taxonomic and functional diversity, we detected potential functional connectivity in railway edges for common semi-natural grassland plants in urban and suburban context. This result can be important for landscape planning and management, especially for countries that are trying to create green networks or infrastructures to link natural areas (Jongman et al., 2004; Zhang and Wang, 2006). Indeed railway edges may be included in these networks in urban contexts. Furthermore, the total length of the railway network worldwide is more than one million kilometres (CIA, 2008), and its edges represent important green areas (e.g., nearly 0.1% of the French area (SNCF, personal communication)). Therefore, the latter could represent an interesting topic for biodiversity conservation in human-dominated landscapes, as already suggested (Jarošík et al., 2011; Le Viol et al., 2008). More precisely, railway edges may contribute, as well as private gardens and green spaces (Vergnes et al., 2012), improving biodiversity in urban environments. Moreover, railway edges plants are mainly herbs and grasses that can be of interest for semi-natural grassland conservation, as already suggested for roads verges (Cousins and Lindborg, 2008).

Given the importance of connectivity for biodiversity conservation, our findings may be of interest to both railway and urban planners. We found that at railway edges, functional connectivity is maintained when the edges are interrupted by stations (i.e., wide, paved surfaces) but not when interrupted by overpasses, which are likely too narrow to retain seeds or for animals to cross. However, to confirm these findings, it would be useful to assess the part of the air flow generated by trains in the functional connectivity we found. Nevertheless we propose that railway edges' functional connectivity in urban context could be improved with vegetated overpasses and stations (that already exist in rural context) or with enlargement of overpass width during railway construction or renovation. Both these options need to be tested and their cost-effectiveness has to be estimated in order to evaluate if they are realistic (SNCF, personal communication). Another solution would be the building of side walls on overpasses (solid parapets) that would play a windbreak function, reduce crosswind effects on train's slipstream and thus could yield a good seed retention system (Barcala and Meseguer, 2007). This solution is technically simple and more realistic than the previous ones. Indeed, side walls already exist for other purposes such as noise reduction. As mowing is necessary for traffic safety reasons, an extensive mosaic management of this vegetation should be beneficial for both plants and animals conservation (Auestad et al., 2010; Noordijk et al.,

2009). Of course all the technical solutions should be tested to assess which (e.g. according to rarity or invasiveness) and how many (richness and abundance) species would benefit from improved connectivity, using for example seed traps. Indeed connectivity may be a problem in the spread of invasive plants (Hansen and Clevenger, 2005). Therefore, improvements in connectivity should always be accompanied by a monitoring of invasive species in the aim of an adaptive management and they may provide an interesting way to help attenuate the negative effects of fragmentation on biotic communities, especially in the urban context.

Acknowledgments

This work was co-funded by the Infrastructure of SNCF (CSC EM) and ANRT (Agence Nationale pour la Recherche Technique). We are grateful to SNCF Engineering for logistical support and to Jean-Pierre Pujols and François Lauzeral for their interest in our work. We also would like to thank Sandrine Pavoine for her invaluable help with the statistical analyses as well as Claire Jouseau and two anonymous reviewers for their helpful comments to the manuscript.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2012.01.041.

References

- Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L., Sanders, N.J., Cornell, H.V., Comita, L.S., Davies, K.F., Harrison, S.P., Kraft, N.J.B., Stegen, J.C., Swenson, N.G., 2011. Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecol. Lett.* 14, 19–28.
- Auestad, I., Rydgren, K., Jongejans, E., de Kroon, H., 2010. *Pimpinella saxifraga* is maintained in road verges by mosaic management. *Biol. Conserv.* 143, 899–907.
- Barcala, M.A., Meseguer, J., 2007. An experimental study of the influence of parapets on the aerodynamic loads under cross wind on a two-dimensional model of a railway vehicle on a bridge. *Proc. Inst. Mech. Eng. Part F – J. Rail Rapid Transit* 221, 487–494.
- Botham, M.S., Rothery, P., Hulme, P.E., Hill, M.O., Preston, C.D., Roy, D.B., 2009. Do urban areas act as foci for the spread of alien plant species? An assessment of temporal trends in the UK. *Divers. Distrib.* 15, 338–345.
- Brown, G.P., Phillips, B.L., Webb, J.K., Shine, R., 2006. Toad on the road: use of roads as dispersal corridors by cane toads (*Bufo marinus*) at an invasion front in tropical Australia. *Biol. Conserv.* 133, 88–94.
- Burton, M.L., Samuelson, L.J., Pan, S., 2005. Riparian woody plant diversity and forest structure along an urban–rural gradient. *Urban Ecosyst.* 8, 93–106.
- Calabrese, J.M., Fagan, W.F., 2004. A comparison–shopper's guide to connectivity metrics. *Front. Ecol. Environ.* 2, 529–536.
- CIA, 2008. The World Factbook. <<http://www.cia.gov/>>.
- Cousins, S.A.O., Lindborg, R., 2008. Remnant grassland habitats as source communities for plant diversification in agricultural landscapes. *Biol. Conserv.* 141, 233–240.
- Debinski, D.M., Holt, R.D., 2000. A survey and overview of habitat fragmentation experiments. *Conserv. Biol.* 14, 342–355.
- Doerr, V.A.J., Barrett, T., Doerr, E.D., 2011. Connectivity, dispersal behaviour and conservation under climate change: a response to Hodgson et al. *J. Appl. Ecol.* 48, 143–147.
- Douda, J., 2010. The role of landscape configuration in plant composition of floodplain forests across different physiographic areas. *J. Veg. Sci.* 21, 1110–1124.
- Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W., Paulißen, D., 1992. Zeigerwerte von Pflanzen in Mitteleuropa. *Scrip. Geobot.* 18, 1–258.
- Ernst, W.H.O., 1998. Invasion, dispersal and ecology of the South African neophyte *Senecio inaequidens* in The Netherlands: from wool alien to railway and road alien. *Acta Bot. Neerl.* 47, 131–151.
- Ewers, R.M., Didham, R.K., 2006. Confounding factors in the detection of species responses to habitat fragmentation. *Biol. Rev.* 81, 117–142.
- Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. *Ann. Rev. Ecol. Syst.* 34, 487–515.
- Gomez, C., Espadaler, X., 1998. Myrmecochorous dispersal distances: a world survey. *J. Biogeogr.* 25, 573–580.
- Grimm, N.B., Faeth, S.H., Golubiewski, N.E., Redman, C.L., Wu, J.G., Bai, X.M., Briggs, J.M., 2008. Global change and the ecology of cities. *Science* 319, 756–760.
- Hansen, M.J., Clevenger, A.P., 2005. The influence of disturbance and habitat on the presence of non-native plant species along transport corridors. *Biol. Conserv.* 125, 249–259.
- Hoyle, M., Cresswell, J.E., 2009. Maximum feasible distance of windborne cross-pollination in *Brassica napus*: a 'mass budget' model. *Ecol. Modell.* 220, 1090–1097.
- IAURIF, 2003. Institute for Planning and Development of the Paris Ile-de-France Region. <<http://www.iaurif.org>>.
- IPNI, 2008. The International Plant Names Index. <<http://www.ipni.org>>.
- Jackson, N.D., Fahrig, L., 2011. Relative effects of road mortality and decreased connectivity on population genetic diversity. *Biol. Conserv.* 144, 3143–3148.
- Jarošík, J., Konvička, M., Pyšek, P., Kadlec, T., Beneš, J., 2011. Conservation in a city: do the same principles apply to different taxa? *Biol. Conserv.* 144, 490–499.
- Jongman, R.H.G., Kulvik, M., Kristiansen, I., 2004. European ecological networks and greenways. *Landscape Urban Plan.* 68, 305–319.
- Kerguelen, M., 2003. Base de Données Nomenclaturales de la Flore de France (BDNFF) version 3.
- Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J.P., Thompson, K., Sonnenschein, M., Poschlod, P., Van Groenendael, J.M., Klimeš, L., Klimešová, J., Klotz, S., Rusch, G.M., Hermy, M., Adriaens, D., Boedeltje, G., Bossuyt, B., Dannemann, A., Endels, P., Götzenberger, L., Hodgson, J.G., Jackel, A.K., Kühn, I., Kunzmann, D., Ozinga, W.A., Römermann, C., Stadler, M., Schlegelmilch, J., Steendam, H.J., Tackenberg, O., Wilmann, B., Cornelissen, J.H.C., Eriksson, O., Garnier, E., Peco, B., 2008. The LEDA traitbase: a database of life-history traits of the Northwest European flora. *J. Ecol.* 96, 1266–1274.
- Klotz, S., Kühn, I., Durka, W., 2002. BIOLFLOR – Eine Datenbank zu biologisch-ökologischen Merkmalen der Gefäßpflanzen in Deutschland. Schriftenreihe für Vegetationskunde. Bundesamt für Naturschutz, Bonn.
- Knapp, S., Kühn, I., Schweiger, O., Klotz, S., 2008a. Challenging urban species diversity: contrasting phylogenetic patterns across plant functional groups in Germany. *Ecol. Lett.* 11, 1054–1064.
- Knapp, S., Kuhn, I., Wittig, R., Ozinga, W.A., Poschlod, P., Klotz, S., 2008b. Urbanization causes shifts in species' trait state frequencies. *Preslia* 80, 375–388.
- Knapp, S., Kuhn, I., Bakker, J.P., Kleyer, M., Klotz, S., Ozinga, W.A., Poschlod, P., Thompson, K., Thuiller, W., Romermann, C., 2009. How species traits and affinity to urban land use control large-scale species frequency. *Divers. Distrib.* 15, 533–546.
- Kowarik, I., von der Lippe, M., 2011. Secondary wind dispersal enhances long-distance dispersal of an invasive species in urban road corridors. *NeoBiota* 9, 49–70.
- Lawton, J.H., 1999. Are there general laws in ecology? *Oikos* 84, 177–192.
- Le Viol, I., Julliard, R., Kerbiriou, C., de Redon, L., Carnino, N., Machon, N., Porcher, E., 2008. Plant and spider communities benefit differently from the presence of planted hedgerows in highway verges. *Biol. Conserv.* 141, 1581–1590.
- Lososová, Z., Chytrý, M., Kuhn, I., Hajek, O., Horakova, V., Pyšek, P., Tichý, L., 2006. Patterns of plant traits in annual vegetation of man-made habitats in central Europe. *Perspect. Plant Ecol. Evol. Syst.* 8, 69–81.
- Marzluff, J.M., Shulenberger, E., Endlicher, W., Alberti, M., Bradley, G., Ryan, C., Simon, U., ZumBrunnen, C., Kowarik, I., 2008. On the role of alien species in urban flora and vegetation. In: *Urban Ecology*. Springer, US, pp. 321–338.
- Matlack, G.R., Monde, J., 2004. Consequences of low mobility in spatially and temporally heterogeneous ecosystems. *J. Ecol.* 92, 1025–1035.
- Mayfield, M.M., Ackerly, D., Daily, G.C., 2006. The diversity and conservation of plant reproductive and dispersal functional traits in human-dominated tropical landscapes. *J. Ecol.* 94, 522–536.
- McDonnell, M.J., Pickett, S.T.A., Groffman, P., Bohlen, P., Pouyat, R.V., Zipperer, W.C., Parmelee, R.W., Carreiro, M.M., Medley, K., 1997. Ecosystem processes along an urban-to-rural gradient. *Urban Ecosyst.* 1, 21–36.
- McKinney, M.L., 2004. Citizens as propagules for exotic plants: measurement and management implications. *Weed Technol.* 18, 1480–1483.
- McKinney, M., 2008. Effects of urbanization on species richness: a review of plants and animals. *Urban Ecosyst.* 11, 161–176.
- Morimoto, J., Kominami, R., Koike, T., 2010. Distribution and characteristics of the soil seed bank of the black locust (*Robinia pseudoacacia*) in a headwater basin in northern Japan. *Landscape Ecol.* 6, 193–199.
- Muratet, A., Machon, N., Jiguet, F., Moret, J., Porcher, E., 2007. The role of urban structures in the distribution of wasteland flora in the Greater Paris area, France. *Ecosystems* 10, 661–671.
- Muratet, A., Porcher, E., Devictor, V., Arnal, G., Moret, J., Wright, S., Machon, N., 2008. Evaluation of floristic diversity in urban areas as a basis for habitat management. *Appl. Veg. Sci.* 11, 451–460.
- Noordijk, J., Delille, K., Schaffers, A.P., Sýkora, K.V., 2009. Optimizing grassland management for flower-visiting insects in roadside verges. *Biol. Conserv.* 142, 2097–2103.
- Ockinger, E., Schweiger, O., Crist, T.O., Debinski, D.M., Krauss, J., Kuussaari, M., Petersen, J.D., Poyry, J., Settele, J., Summerville, K.S., Bommarco, R., 2010. Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. *Ecol. Lett.* 13, 969–979.
- Okubo, A., Levin, S.A., 1989. A theoretical framework for data-analysis of wind dispersal of seeds and pollen. *Ecology* 70, 329–338.
- Pasquet, R.S., Peltier, A., Hufford, M.B., Oudin, E., Saulnier, J., Paul, L., Knudsen, J.T., Herren, H.R., Gepts, P., 2008. Long-distance pollen flow assessment through evaluation of pollinator foraging range suggests transgene escape distances. *Proc. Natl. Acad. Sci. USA* 105, 13456–13461.
- Pellissier, V., Roze, F., Aguejard, R., Quenol, H., Clergeau, P., 2008. Relationships between soil seed bank, vegetation and soil fertility along an urbanisation gradient. *Appl. Veg. Sci.* 11, 325–334.
- Pennington, D.N., Hansel, J.R., Gorchov, D.L., 2010. Urbanization and riparian forest woody communities: diversity, composition, and structure within a metropolitan landscape. *Biol. Conserv.* 143, 182–194.

- Pyšek, P., 1998. Alien and native species in Central European urban floras: a quantitative comparison. *J. Biogeogr.* 25, 155–163.
- R Development Core Team, 2009. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Roy, V., de Blois, S., 2006. Using functional traits to assess the role of hedgerow corridors as environmental filters for forest herbs. *Biol. Conserv.* 130, 592–603.
- Schleicher, A., Biedermann, R., Kleyer, M., 2011. Dispersal traits determine plant response to habitat connectivity in an urban landscape. *Landscape Ecol.*, 1–12.
- Stenhouse, R.N., 2004. Fragmentation and internal disturbance of native vegetation reserves in the Perth metropolitan area, Western Australia. *Landscape Urban Plan.* 68, 389–401.
- Taylor, P.D., Fahrig, L., Henein, K., Merriam, G., 1993. Connectivity is a vital element of landscape structure. *Oikos* 68, 571–573.
- Tewksbury, J.J., Levey, D.J., Haddad, N.M., Sargent, S., Orrock, J.L., Weldon, A., Danielson, B.J., Brinkerhoff, J., Damschen, E.I., Townsend, P., 2002. Corridors affect plants, animals, and their interactions in fragmented landscapes. *Proc. Natl. Acad. Sci. USA* 99, 12923–12926.
- Thomas, C.D., 2000. Dispersal and extinction in fragmented landscapes. *Proc. Roy. Soc. Lond. Ser. B – Biol. Sci.* 267, 139–145.
- Tikka, P.M., Hogmander, H., Koski, P.S., 2001. Road and railway verges serve as dispersal corridors for grassland plants. *Landscape Ecol.* 16, 659–666.
- Tremblay, M.A., St. Clair, C.C., 2009. Factors affecting the permeability of transportation and riparian corridors to the movements of songbirds in an urban landscape. *J. Appl. Ecol.* 46, 1314–1322.
- Vallet, J., Daniel, H., Beaujouan, V., Roze, F., Pavoine, S., 2010. Using biological traits to assess how urbanization filters plant species of small woodlands. *Appl. Veg. Sci.* 13, 412–424.
- Vergnes, A., Viol, I.L., Clergeau, P., 2012. Green corridors in urban landscapes affect the arthropod communities of domestic gardens. *Biol. Conserv.* 145, 171–178.
- Vittoz, P., Engler, R., 2007. Seed dispersal distances: a typology based on dispersal modes and plant traits. *Bot. Helv.* 117, 109–124.
- Von der Lippe, M., Kowarik, I., 2007. Long-distance dispersal of plants by vehicles as a driver of plant invasions. *Conserv. Biol.* 21, 986–996.
- Wehling, S., Diekmann, M., 2009. Importance of hedgerows as habitat corridors for forest plants in agricultural landscapes. *Biol. Conserv.* 142, 2522–2530.
- Wilcove, D.S., McLellan, C.H., Dobson, A.P., 1986. Habitat fragmentation in the temperate zone. In: Soulé, M.E. (Ed.), *Conservation Biology*. Sinauer Associates, pp. 237–256.
- Williams, N.S.G., Schwartz, M.W., Veski, P.A., McCarthy, M.A., Hahs, A.K., Clemants, S.E., Corlett, R.T., Duncan, R.P., Norton, B.A., Thompson, K., McDonnell, M.J., 2009. A conceptual framework for predicting the effects of urban environments on floras. *J. Ecol.* 97, 4–9.
- Winkler, E., Fischer, M., 2001. The role of vegetative spread and seed dispersal for optimal life histories of clonal plants: a simulation study. *Evol. Ecol.* 15, 281–301.
- Zhang, L.Q., Wang, H.Z., 2006. Planning an ecological network of Xiamen Island (China) using landscape metrics and network analysis. *Landscape Urban Plan.* 78, 449–456.
- Zobel, M., 1997. The relative role of species pools in determining plant species richness. An alternative explanation of species coexistence? *Trends Ecol. Evol.* 12, 266–269.