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Evaluation of landscape connectivity at community level using satellite-derived NDVI

Audrey Muratet · Romain Lorrillière · Philippe Clergeau · Colin Fontaine

A. Muratet (&)

ODBU, Observatoire Départemental de la Biodiversité Urbaine, Direction de la Nature, des Paysages et de la Biodiversité, Conseil Général de la Seine-Saint-Denis, Hôtel du Département, 93006 Bobigny Cedex, France e-mail: amuratet@cg93.fr

R. Lorrillière P. Clergeau C. Fontaine

UMR 7204 CNRS-MNHN-UPMC, Conservation des Espèces, Restauration et Suivi des Populations, Muséum National d'Histoire Naturelle, 61 Rue Buffon, 75005 Paris, France e-mail: lorrilliere@mnhn.fr

P. Clergeau

e-mail: clergeau@mnhn.fr

C. Fontaine

e-mail: cfontaine@mnhn.fr

heterogeneity of matrix resistance estimated by the normalised difference vegetation index (NDVI), and quantifying the link strength between patches with the shortest path and flow metrics. We assessed the fit of these connectivity predictions with empirical data on plant communities embedded in an urban matrix. Our results indicate that the best fit with the empirical data is obtained when the connectivity is estimated with the flow metric and takes into account the matrix heterogeneity. Overall, our study helps to estimate the landscape connectivity of urban areas and makes recommendations for ways in which we might optimise landscape planning with respect to conservation of urban biodiversity.

Keywords Graph theory Flux Habitat fragmentation Least-cost path Network Permeability Plant community Satellite imagery Urban ecology

Abstract Landscape connectivity, defined as the degree to which the landscape facilitates or impedes movement among resource patches, has been considered to be a key issue for biodiversity conservation. However, the use of landscape connectivity measurements has been strongly criticised due to uncertainties in the methods used and the lack of validation. Moreover, measurements are typically restricted to the population level, whereas management is generally carried out at the community level. Here, we used satellite imagery and network metrics to predict the landscape connectivity at community level for seminatural herbaceous patches in an urban area near Paris (France). We tested different measurement methods, both taking into account and ignoring the spatial

Introduction

As a consequence of increasing anthropic pressures, the total area of natural habitat is shrinking and becoming increasingly fragmented into numerous small remnant patches (Grimm et al. 2000). Conservation theory predicts first that large habitat patches have more species than small ones, and second that connected patches have more species than isolated ones (MacArthur and Wilson 1967). In recent decades, this second prediction became a central issue for biodiversity conservation and management, leading Merriam (1984) to introduce for the first time the concept of landscape connectivity and Crooks and Sanjayan (2006) to propose the term 'connectivity conservation'. This issue is particularly relevant for biodiversity conservation in urban areas. Urbanisation is one of the most important causes of habitat loss and fragmentation and is often long-lasting. From 2000 to 2006, France has experienced a 3 % increase in urban areas, a 0.2 % decrease in agricultural areas and a 0.04 % decrease in natural areas (SOeS 2010). Vegetation is suppressed over large land parcels and the percentage of fully-impervious surfaces, such as pavements, asphalt, or buildings ranges from well over 50 % at the urban core to less than 20 % at the fringe of urban expansion (McKinney 2002). Preserving biodiversity in urban areas is an important challenge because despite high levels of fragmentation, urban areas can act as a refuge for some species (Saure 1996; Von der Lippe and Kowarik 2008). Moreover, there is now evidence for the positive effect of urban biodiversity on human health and well-being (Tzoulas et al. 2007). As preserving large contiguous areas is often difficult in an urban context, management options have to consider ways of assessing and potentially improving links between patches to maximise biodiversity conservation. Indeed, gene flows, migration, local extinction, recolonization, and thus community structure and stability will depend on individual movements between patches (Campbell Grant et al. 2007). As claimed by Angold et al. (2006), an essential first step towards managing biodiversity in urban environments is a fuller understanding of the interplay between landscape characteristics and local factors that affect urban biodiversity.

Landscape connectivity is defined as the degree to which the landscape facilitates or impedes individual movements between resource patches (Taylor et al. 1993). Numerous connectivity measures exist based on (1) the physical structure of a landscape, i.e. size, shape and location of resource patches and on (2) a continuum in the degree of information on species dispersal ability and on the nature of the intervening matrix (see Tischendorf and Fahrig 2000; Calabrese and Fagan 2004 for proposed classification). Small and large scale studies show that matrix quality is an important driver of the ecological dynamics of numerous taxa in fragmented landscapes (Fahrig 2007; Prugh et al. 2008; Watling et al. 2011).

Matrix resistance to species movements has usually been estimated by experts based on Landsat-derived vegetation or land-use classifications (Adriaens et al. 2003; Sun et al. 2006; Magle et al. 2009; Theobald et al. 2012) or empirical knowledge on habitat-use and/or ease-of-dispersal through different habitat types (Ricketts 2001; Ray et al. 2002; Castellon and Sieving 2006; Umetsu and Pardini 2006). Such approaches were typically species-specific, leading to biological validations of connectivity metrics at the population level (Gonzales and Gergel 2007; Baldwin and de Maynadier 2009; Conrad et al. 2012). However, management choices and restoration programs are more often focused at the community level (Hodgson et al. 2009), and the aim of urban conservation is not limited to a few emblematic species but rather to preserving stable and robust communities composed of common species (Gaston 2011). Such incentives to adapting connectivity measurement to the community scale are scarce (but see Compton et al. 2007; Schleicher et al. 2011; Shanahan et al. 2011) and biological validation at the community scale is still lacking.

The relevant ecological level for landscape connectivity has been debated at length and numerous ecologists claim that landscape connectivity should be limited to the population level (Prevedello and Vieira 2010). Doerr et al. (2011) argued that responses to landscape connectivity may not be as species-specific as claimed. Within communities, species with similar life history traits may have been selected or filtered by their shared environments. For example, herbaceous

species commonly found in urban areas tend to be highly mobile, with short life-cycles and should thus reflect the recent dynamic of habitat changes.

In this paper, we propose a new method to assess landscape connectivity based on the normalised difference vegetation index (NDVI). We aim to assess landscape connectivity on a large scale by a new approach validated at the community level. We estimated matrix resistance using the NDVI, which is commonly used in ecological studies, but has never before been used to assess connectivity. In urban areas, as the matrix quality goes from fully-impervious to fully-vegetated surfaces, we hypothesised that vegetation cover could provide an easy approximation of matrix resistance to the dispersal ability of various plant species. The NDVI, estimated from satellite imagery, is strongly related to the extent of vegetation cover (Purevdorj et al. 1998) and can thus provide the data needed to characterise the landscape heterogeneity (Kerr and Ostrovsky 2003).

We assessed our approach by studying a network of patches of semi-natural herbaceous habitats, embedded in a large urbanised landscape. Networks structures and habitat availability metrics are two recent and complementary approaches for analysing landscape connectivity (Saura and Rubio 2010). We tested whether a connectivity measurement based on a modelling of individual movements and taking into account the spatial variability of matrix resistance from NDVI data, offered a better explanation of the variation in community composition of herbaceous patches than a connectivity measurement based solely on distances between patches. We further tested two network metrics for the quantification of the link strength between patches: shortest path and maximum flow. Then, we calibrated the predicted connectivities with biological data on plant communities. We expected the similarity in species composition between pairs of habitat patches to be higher as the link between the two habitat patches is stronger. Finally, we discussed our results from both a fundamental perspective on connectivity measurements and an applied perspective on how to deliver relevant information to assist decision-making for urban planners.

Materials and methods

Study area

We selected a large, densely populated urbanised area of 236 km² bordering the east of Paris (4854⁰N, 229⁰W, with 5,855 people/km² versus 95 people/km² in France, INSEE 1999) in the Seine-Saint-Denis district. The climate is oceanic with continental trends (mean annual temperature 11.7 C and annual rainfall: 641 mm). We analysed landscape connectivity for the patches of semi-natural herbaceous habitat only (i.e. unmanaged and uncultivated habitat composed of spontaneous plants), enabling us to connect patches providing similar living conditions for herbaceous plants. We thus used as a source layer a geographic grid of 15 9 15 m cells that contained 446 seminatural herbaceous patches within our chosen territory (National Botanical Conservatory of the Paris Basin, CBNBP (2008), see Fig. 1), breaking down as meadows (43.3 %), wastelands (40.9 %) and calcareous lawns (1.4 %). The remaining 14.4 % corresponded essentially to small wooded spaces (13.6 %) and to humid (0.3 %) or managed (0.5 %) zones embedded in herbaceous patches. Patch area was on average 2.65 ha (ranging from 0.04 to 206 ha) and the total area covered 5 % of the total territory. This source layer map was created from photo-interpretation and land surveys by the National Botanical Conservatory of the Paris Basin (CBNBP 2008).

Estimation of patch links

We estimated the presence of links between patches using two methods. The first one considered that matrix resistance was homogeneous throughout the landscape, hereafter referred to as homogeneous matrix. The second took into account the spatial variability of matrix resistance, hereafter heterogeneous matrix. Both methods allowed us to predict the presence or absence of links between pairs of patches, resulting in a network of patches, referred to hereafter as a connectivity network, and illustrated as a graph composed of nodes (habitat patches) and links. For each method, we then used two metrics to quantify link strengths between each pair of habitat patches,

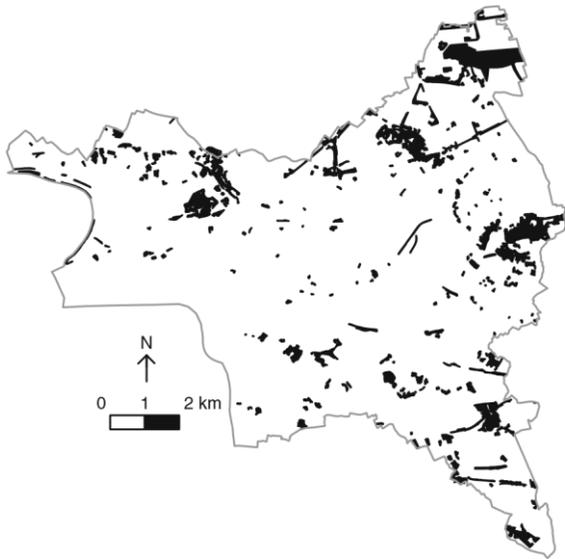


Fig. 1 Distribution of the 446 semi-natural herbaceous patches in the Seine-Saint-Denis district (CBNBP 2008) based, respectively, on shortest path and maximum flow.

Homogeneous matrix

We estimated the presence of links between habitat patches based on Euclidean distances between their edges. A link between two patches was registered when the Euclidean distance between them was inferior to D_{max} , i.e., the maximal distance travelled from one patch to another. Several D_{max} values were tested, ranging from 250 m to 3 km in 50 m steps. This includes long-distance seed dispersal observed in grasslands (Soons et al. 2004) and more generally in a panel of habitats (see the review of Thomson et al. 2011).

Heterogeneous matrix

We estimated the presence of links between patches by modelling individual movements. Model inputs were both a source layer, i.e., the herbaceous patches, and a resistance layer, i.e., the heterogeneous matrix corresponding to the resistance of the urban matrix surrounding herbaceous patches. Resistance values were normalised difference vegetation index (NDVI, IAURIF 2000) data estimated from Landsat 7 Thematic

Mappersatelliteimageryrecordedon28thAugust2000. NDVI is derived from the red (q_R) and near-infrared (q_N) wavelengths (Myneni et al. 1995):

$$NDVI = \frac{q_N - q_R}{q_N + q_R}$$

The formula is based on the fact that chlorophyll absorbs q_R whereas the mesophyll leaf structure scatters q_N . NDVI values thus range from -1 to 1 and were classified in 13 classes ranging from zero (dense vegetation) to 12 (concreted). Each 15 × 15 m cell of the resistance layer (i.e., heterogeneous matrix) had a resistance value to individual movements corresponding to its NDVI class.

The movement of 100 individuals per boundary cell of each habitat patch (named in this case source patch) was simulated by a stochastic individual model.

Individuals $I_{xy(s)}$, were characterised by their position in the urban landscape, x, y . Each individual was independent but the rules of their movement through the heterogeneous matrix were identical. An individual moved one cell per step following a recursive procedure with a maximum number of steps (S_{max}).

While $s_i \leq S_{max}$, the next position $I_{xy(s+1)}$ was defined by a function of neighbourhood choice. This function can be described in three steps; (1) The eight $I_{xy(s)}$ neighbourhoods (excluding already-visited cells and departure patch cells) were sorted according to their resistance values (the order of the neighbourhoods that have the same resistance is randomized) and a rank was assigned to each; (2) The next cell $I_{xy(s+1)}$ was chosen from a truncated Poisson distribution ranging from 1 to the number of available cells; (3) One cell was chosen following a uniform distribution, to be the next step, $I_{xy(s+1)}$. Individual movement simulation ended: (1) when the individual I found a new habitat patch, dispersal was a success and a link was observed between source and target patches; (2) when $s_i = S_{max}$, dispersal failed, no link was created by this individual. Different scenarios were computed for various S_{max} values, ranging from 50 to 600 steps. Even if we cannot directly compare these values to D_{max} , we could assert that they contain known long-distance seed dispersal as above.

Shortest path

We based our first method used to quantify link strength among patches on the shortest path metric, i.e. the shortest path between two patches based on the network of links between patches. We measured Euclidean distances between the edges of these connected patches. We used the `shortest.paths` function of the `igraph` library from R software (West 1996) to calculate the shortest path between all patches with either direct or indirect links, using other patches as stepping stones. We obtained a shortest path distance matrix for each D_{\max} and S_{\max} value. For unconnected (directly and indirectly) patches, the distance given was infinite.

Maximum flow

We based our second method on the concept of flow that referred to physical flow as electrical or water distribution. In our case, we assessed the number of independent paths (direct and indirect) linking any two habitat patches. We used the `maxflow` function of the `sna` library (Butts 2008) from R software, to obtain a maximum flow matrix for each D_{\max} and S_{\max} value. For unconnected patches the flow was zero. We gave the same weight to all links of the network.

Fit of the estimated landscape connectivity to the empirical data

For the four methods used to estimate links between patches (two methods to estimate the presence of links and time two methods to quantify the strength of links among patches), we selected D_{\max} or S_{\max} values that fit best with the empirical data as follows:

Empirical data

We used a sample of 21 habitat patches for which floristic data was collected between 2001 and 2002 by the CBNBP (2008). A minimum of four quadrats of 100 m² (mean = 7 and max = 15) were inventoried in each patch of semi-natural herbaceous habitat sampled. In each quadrat, all wild (indigenous and naturalised, see Richardson et al. 2000 for a definition) vascular species present were recorded.

Biological distance between patches—which measures the dissimilarity in species composition—was assessed via semi-metric Bray–Curtis measurements based on mean abundance-based matrices using the `vegan` library from R software (Oksanen et al. 2005). To avoid bias due to mosaic community composition (essentially in wooded areas), we removed from the analysis shrubs and trees that could affect our results by artificially increasing dissimilarities between habitat patches.

Fit of the estimated landscape connectivity

The fit of connectivity networks observed using the four methods described above to empirical data were assessed by Pearson correlation coefficients, calculated between biological distances and link strength measurements (shortest path or flow) for each D_{\max} and S_{\max} value. We selected the four connectivity networks whose dispersal potential showed the highest correlation.

Structure of the best-fitting connectivity networks

We used graph theory (Bunn et al. 2000; Urban and Keitt 2001; Galpern et al. 2011 for a review) to analyse the structure of the best-fitting connectivity networks. For each of the four methods, we calculated the connectance (C) of the best-fitting network as

$$C = L / S(S - 1) = 2P$$

with L being the number of links and S the number of patches.

We also calculated the number of components, i.e. disconnected sets of linked patches. These two indices reflect two global landscape connectivity aspects: the density of the links within the network and its degree of fragmentation.

We then focused our analysis on the main components of the best-fitting networks. For each, we calculated their size (number of patches) and connectance.

Fig. 2 Correlation coefficients between strength of patch links (a, b shortest paths or c, d flows) and biological distances among patches on the network based on a homogeneous matrix for various values of D_{\max} (a and c) and on the heterogeneous network for various values of S_{\max} (b and d). Correlation coefficient not different from 0 are plotted with empty symbols. Highest correlation are circled

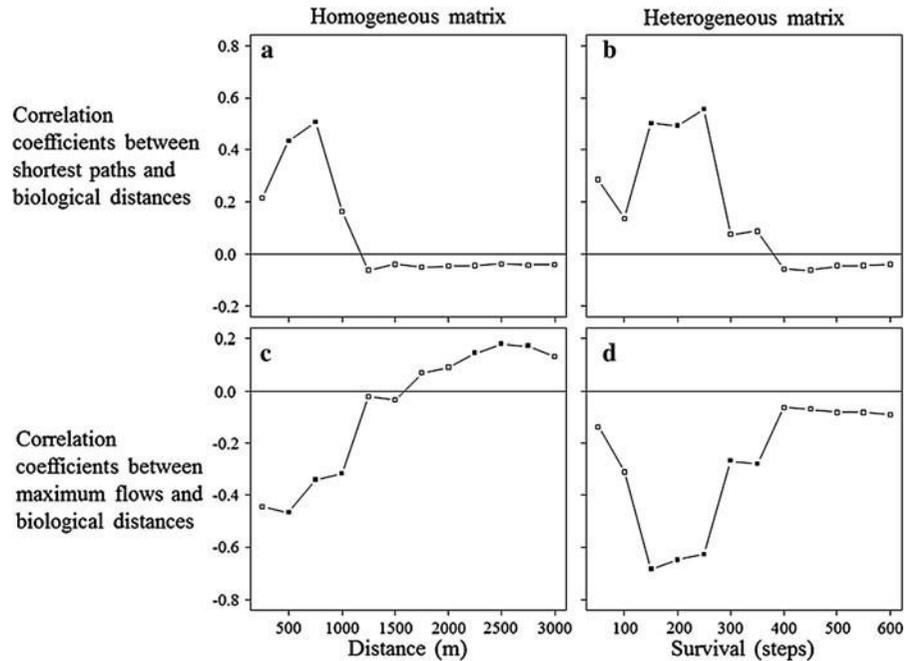


Table 1 Structural characteristics of the best fitting networks

Methods		Connectance	Total no. of components	No. of components
Matrix type	Link strength			□10
Homogeneous	Shortest path	0.020	23	4
Homogeneous	Maximum flow	0.013	54	11
Heterogeneous	Shortest path	0.014	15	4
Heterogeneous	Maximum flow	0.011	27	4

Results

To calibrate our model, we used data on the composition of plant communities in 21 sites. At all we recorded 240 species and on average, 50 (± 21) species were recorded per study site. The most frequently encountered species were cock's-foot (*Dactylis glomerata*, 114 observations in 18 sites), false oat-grass (*Arrhenatherum elatius*, 98 observations in 17 sites), creeping thistle (*Cirsium arvense*, 90 observations in 20 sites) and hawkweed oxtongue (*Picris hieracioides*, 88 observations in 18 sites). More generally, among the different species observed, the most frequent families encountered were Asteraceae (46 species, 27 % of observations), Poaceae (30 species, 23 % of observations), Fabaceae (25 species, 12 % of observations) and Apiaceae (11 species, 7 % of observations).

For each of the four methods used, we observed a clear correlation pick between biological distances and link strengths (Fig. 2). This indicated that for simulated dispersal distances lower than the pick, some connections among patches were missing and that for simulated dispersal distances higher than the pick, some connections among patches were not supported by the empirical dataset. Interestingly, for both homogeneous and heterogeneous matrices, the use of maximum flows to quantify link strength tended to reduce the dispersal potential for which the highest correlation was observed, from, respectively, $D_{\max} = 750$ m to $D_{\max} = 500$ m (Fig. 2a, c), and from $S_{\max} = 250$ steps to $S_{\max} = 150$ steps (Fig. 2b, d).

Regarding the structure of the corresponding four best-fitting networks, the use of the maximum flow methods led to less-linked networks with a higher

number of components (Table 1; Fig. 3c, d). In particular, the best-fitting network in a homogeneous matrix with maximum flow method was highly fragmented into numerous small sets of linked patches (Table 1; Fig. 3c). By contrast, the best-fitting networks we obtained with the three other methods were clearly structured into four main components

which tended to be higher when using the homogeneous matrix (mean = 0.14 versus 0.08 for the heterogeneous matrix, see Table 2B). It is worth noting that the estimation of link-strength by flows increased the fit of network topology to the species composition of plant communities when using the heterogeneous matrix (shortest path: $r_{\max} = 0.56$, flow: $r_{\min} = -0.68$; Fig.

Table 2 Structural characteristics of the four main components of the best fitting networks regarding the number of patches they include (A) and their connectance (B)

Component	No. of patches				Overlap in patch composition					
	Homogeneous		Heterogeneous		hs vs. hf	hs vs. Hs	hs vs. Hf	Hs vs. Hf	Hs vs. hf	Hf vs. hf
	s. path	m. flow	s. path	m. flow						
A										
1	190	80	216	183	1	1	1	1	1	1
2	83	52	89	83	0	1	1	1	0	0
3	77	43	82	77	0	1	1	1	0	0
4	33	38	33	33	0	1	1	1	0	0
Component	Connectance				Overlap in link composition					
	Homogeneous		Heterogeneous		hs vs. hf	hs vs. Hs	hs vs. Hf	Hs vs. Hf	Hs vs. hf	Hf vs. hf
	s. path	m. flow	s. path	m. flow						
B										
1	0.06	0.09	0.03	0.03	1	0.82	0.97	1	0.73	0.72
2	0.13	0.15	0.08	0.07	0	0.87	0.99	1	0	0
3	0.09	0.21	0.07	0.06	0	0.84	0.96	1	0	0
4	0.24	0.13	0.15	0.13	0	0.91	0.97	1	0	0

Hs heterogeneous matrix and shortest path method; hs homogeneous matrix and shortest path method; Hf heterogeneous matrix and maximum flow method; hf homogeneous matrix and maximum flow method

(Table 1; Fig. 3a, b and d).

When focussing on the four main components of the best-fitting networks, the overlap in patch composition of each component was always equal to one, except for the comparison involving the method coupling the homogeneous matrix with the maximum flow (Table 2A). This indicated that except for this last method, the predicted connectivity networks were very similar on a coarse scale, and all of them identified the same four main components.

On a finer scale, both the heterogeneous matrix and the shortest path methods tended to predict a higher number of patches per component (Table 2A). The four main components also differ in their connectance,

whereas it tended to reduce the network fit when using the homogeneous matrix (shortest path: $r_{\max} = 0.51$, flow: $r_{\min} = -0.47$, Fig. 2a, c). This highlighted the fact that, on a fine scale, the density of links between patches can profoundly affect our estimation of landscape connectivity and that the use of heterogeneous matrix and maximum flow methods appears to generate a more robust and realistic estimate of landscape connectivity.

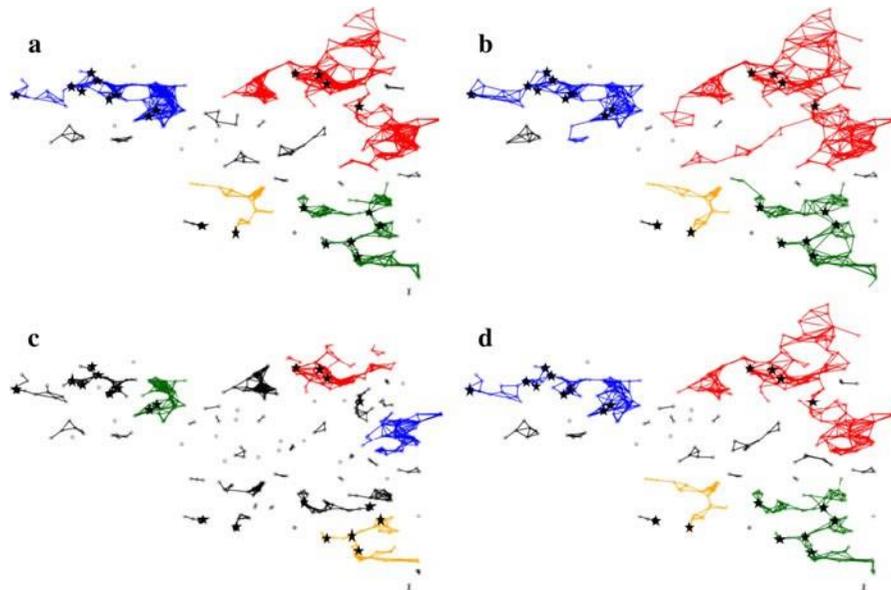


Fig. 3 Network structure obtained with the homogeneous matrix (a, c) and the heterogeneous matrix (b, d) for, respectively, D_{\max} and S_{\max} showing the highest correlation value between biological distances and shortest paths (a, b) or flows (c, d) (see Fig. 2). Thus a network obtained with the homogeneous matrix for $D_{\max} = 750$ m, b network obtained with the heterogeneous matrix for $S_{\max} = 250$ steps, c network obtained with the homogeneous matrix for $D_{\max} = 500$ m, and d network obtained with the heterogeneous matrix for $S_{\max} = 150$ steps. Habitat patches are represented by points and links among patches by lines. Black stars corresponded to the 21 habitat patches with floristic data. The four main components were colourized in red, blue, green, and orange in decreasing size order. (Color figure online)

Discussion

Landscape connectivity at the community scale

Our study highlights important findings for both fundamental and applied aspects of landscape connectivity. Regarding fundamental aspects, we have shown that landscape connectivity is related to the species composition of communities. Landscape connectivity

has been used in a variety of ways in the literature but to date has mostly been restricted to population level studies (Tischendorf and Fahrig 2000 for a review). Moreover, biological validations were scarce at population level and absent at the community level. However, we found a strong influence from landscape connectivity on the species composition of the plant community we studied, indicating that strongly-linked patches exhibit highly similar species composition. These findings could be dependent of three restrictions we made. First, we did not study managed habitats like urban lawns, which could be artificially closed in terms of plant composition because they are subject to common management practices with a strong impact on community composition. Second, we did not take into account ornamental plants in the inventories that are more dependent on management practices than natural processes. Third, we focused our study on a homogeneous habitat to be coherent with the Doerr et al. (2011) hypothesis that species in a given ecological community with broadly similar life-histories may have similar movement behaviours as responses to their shared environments.

Contribution of matrix resistance

Our results further suggest that the density of paths between patches is an important aspect of landscape connectivity that needs to be accounted for to produce more precise and robust estimations of link strength. Whereas most studies to date use shortest path or least resistance path to assess the link strength between patches (Urban and Keitt 2001; Adriaensen et al. 2003; Pascual-Hortal and Saura 2006; Beier et al. 2009; Sawyer et al. 2011 for a review), we also used flows (McRae et al. 2008). Flow measurements have rarely

been used in connectivity studies except by McRae et al. (2008), who applied this method to predict gene flows and Theobald et al. (2012) who applied flow measurement to estimate the connectivity of natural landscapes at regional and continental levels. Contrary to shortest path methods that are related to distances, flows are based on the number of independent paths linking two patches, and are thus sensitive to how densely linked the patches are. Estimating the density of links by measuring the flow between patches produced contrasting effects on the estimation of landscape connectivity based on the homogeneous and heterogeneous matrices. While the best-fitting connectivity network based on heterogeneous matrices did not differ strongly between shortest path and flows methods, the best-fitting connectivity network based on homogeneous matrices were heavily influenced by the method used to estimate link strengths. These results indicate that connectivity measurements based on a homogeneous matrix are efficient at finding which patches are directly or indirectly linked, but tend to overestimate the number of direct links between them. Taking into account spatial variability of the matrix resistance appears to produce a more realistic pattern of patch linkage, which is robust for both shortest-path and flow measurements. These results were in accordance with the mounting evidence suggesting that the matrix can mediate the strength and nature of connectivity effects in fragmented landscapes, as shown on roe deer (Coulon et al. 2004), prairie dogs (Magle et al. 2009) and on a range of terrestrial animals (see meta-analyses of Prugh et al. 2008; Watling et al. 2011). The use of the graph theory has rapidly become the common tool to estimate landscape connectivity (see the reviews of Galpern et al. 2011; Rayfield et al. 2011) and our study provides a new contribution to its efficiency to estimate connectivity on the broad spatial-scale.

Applications

Our study also brings valuable findings to the applied side of landscape connectivity. NDVI has mainly been used in research on temporal and spatial trends of variation in vegetation distribution, productivity and dynamics (see the review of Pettorelli et al. 2005). We

showed that for urban areas, NDVI can be used to estimate the matrix resistance, validating the assertion of Kerr and Ostrovsky (2003) that NDVI can be an indicator of urban landscape heterogeneity. This is particularly interesting as NDVI provides a precise and standardised measurement and is easily available over

large areas. As claimed by Beier et al. (2011), ecological connectivities remain poorly studied on large spatial scales, such as a region or a country. Our approach could help to develop tools to measure, map, and understand connectivity of communities at these scales. Finally, our work produces a clear view of the connectivity of seminatural herbaceous habitats in the Seine-Saint-Denis district and enables us to bring landscape-scale considerations into conservation. Our study should help managers and stakeholders to prioritize on several

levels. The first is for site protection, by locating patches of semi-natural herbaceous habitat essential to maintain landscape connectivity. In a fragmented landscape with a strongly heterogeneous matrix as studied here, movements of individuals are strongly driven by matrix permeability. As a result, individuals will often not reach the resource patches that would provide the best returns (Belisle 2005; Fahrig 2007) but will reach the more accessible patches, whatever their quality. A second prioritization would be site acquisition, by identifying blocking points where new patches would be more beneficial for restoring landscape connectivity. In the territory studied, the network that was most consistent with biological data was composed of four large components mainly distributed at the margin of the territory (Fig. 3d). These main components could be reconnected by the creation of relay (stepping stones) patches between them or by making the landscape more

permeable at the blocking points. The main components might also be managed separately, using local connectivity metrics. In order to improve local component robustness, we recommend the reinforcement of weak links by a densification of possible paths and/or the creation of relay patches. This network was also composed of 11 small components that were more isolated in the urban matrix primarily situated in the centre of the territory, separated by barriers which would

need to be broken in order to reconnect communities and thus species populations. For these components, the implications were more local and reconnection was more problematic. We should, however, keep in mind that connectivity is not the only conservation solution and should be complemented by improvements to habitat quality and quantity (Hodgson et al. 2011).

Perspectives

Our work highlights several perspectives. To facilitate the application of such landscape connectivity assessments to the management of urban ecosystems, we need to develop scenario-based approaches. For this to be achieved, we must develop algorithms capable of predicting links between patches based on matrix resistance faster than individual-centred models, the latter being highly computationally intensive. Another aspect of our work that deserves further attention is the use of flows to estimate link strengths. In this work, flows between patches were considered as binary (linked or not). It could be improved by integrating a quantification of flow for each link. Such quantified flows could easily be predicted by models and may increase the explanatory power of such networks. As shown by Saura and Rubio (2010) we highlighted with an empirical example in a fragmented landscape the contribution of flux (number of independent links) to the overall connectivity contribution for species with various dispersal abilities. Further, we highlighted effects of landscape connectivity on herbaceous community composition; however, the dispersal modes vary among species. In our study, the modes of dispersion (Kleyer 1995) were in majority either passive via autochory and anemochory (54 % of observations) or active via zoochory and anthropochory (44 % of observations). Future analysis should explore possible differences between such plant guilds as the parameter defining landscape connectivity for each guild might be different. Finally, research is needed to evaluate this tool on other fragmented landscapes such as cultivated areas, on other groups that are more or less mobile such as insects or small mammals and also at different time scales to estimate the effect of landscape heterogeneity history and its prediction power on actual connectivity.

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