

# The Role of Urban Structures in the Distribution of Wasteland Flora in the Greater Paris Area, France

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## ABSTRACT

Wastelands are likely to host a significant part of urban floristic diversity but have received limited attention because they are not considered interesting green zones. Here, we explore the potential role of wastelands in maintaining urban biodiversity to help define effective urban management plans. We quantified floristic diversity in 98 wasteland sites of Hauts-de-Seine, one of the most densely populated areas in France, and characterized the environmental parameters and spatial distribution of sites to identify some of the factors that influence plant species composition and to explore the impact of urban environment on the floristic interest of wastelands. Their floristic richness represented 58% of the total richness observed in the whole study area. Site richness depended on site area (the largest sites were the richest) and site age, with a maximum in sites of intermediate age

(4–13 years). In the largest sites only (>2,500 m<sup>2</sup>), the floristic distance among sites was positively correlated with geographic distance, which suggests that migration of species among large sites partly controls local floristic composition. In contrast, the environmental distance among sites was not correlated with floristic distance. Finally, we showed that the presence of collective and individual dwellings within 200 m of a wasteland decreased its floristic rarity, whereas the presence of rivers or ponds increased it. We derive several recommendations to optimize the management of wastelands with respect to conservation of urban biodiversity.

**Key words:** Land use pattern; Indigeneity; Hauts-de-Seine; Isolation by distance; Plant diversity; Rarity; Urbanization.

## INTRODUCTION

Conservation policies in urban zones usually target relicts of natural landscapes, such as wetlands or woodlands. In contrast, artificial urban habitats are not considered interesting green zones by most city-dwellers (Sukopp and Werner 1987). In particular, wastelands, defined as abandoned lands

where plant species grow without human control, are frequently neglected in conservation plans. However, despite their often-negative image, they can be of importance due to their high floristic diversity (Maurer and others 2000; Zerbe and others 2003; Herbst and Herbst 2006). The presence of wastelands in cities may thus contribute significantly to the total biodiversity in urban areas, although the extent of their role is poorly documented. Thus, studying wastelands is of primary concern to assess their role in maintaining

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urban biodiversity and to define effective urban management plans.

Although the high floristic diversity of wastelands is now relatively well documented, very little is known regarding the mechanisms that control the distribution of flora in this habitat; this fundamental information should be accounted for in conservation strategies. As in many human-disturbed habitats, species composition in urban wastelands is likely influenced by (1) biotic and abiotic environmental conditions (soil, light, humidity, interspecific competition...), (2) the pool of species able to colonize from neighboring (wasteland or non-wasteland) sites, (3) the barriers preventing pollen/seed flow among sites, and (4) the frequency and intensity of human-induced disturbance. Wastelands are subject to various development pressures (Harrison and Davies 2002), and their life span is highly variable but generally short. In the short to mid-term, wastelands are partly protected from human-induced disturbance by their negative image, which may favor biodiversity. However, wastelands can also be short-lived habitats whose life span is defined by the necessity to construct new buildings or parks. The succession of local extinctions and colonizations of newly vacant sites from neighboring sites may thus create metacommunity dynamics in urban wastelands. Depending on which factors exert the strongest influence, plant species composition can be spatially autocorrelated (for example, if among-site dispersal is possible but limited in space) or completely patchy (for example, with little among-sites dispersal, strong effect of local environments, or influence of local human pressure only). Unraveling the relative importance of biological interactions, dispersal limitation, and environmental determinism in inducing differences in species composition among sites is a central issue in plant ecology (Hurtt and Pacala 1995; Whitfield 2002).

In the present study, we quantify floristic diversity in approximately 100 wastelands of the Greater Paris area, and for the first time explore the role of some of the human and environmental factors controlling their floristic composition, to evaluate the consequences for the conservation of urban biodiversity. Wasteland floristic diversity was measured via species richness, species rarity and indigeneity. We described the characteristics of wasteland sites (spatial distribution, floristic diversity, age, and area) in one of the most urbanized zones of France and used data from the Land Use Pattern to address the following questions:

- (1) What is the influence of the abiotic environment on the floristic diversity of wastelands? To address this, we compared matrices of floristic distances to matrices of environmental distances between wasteland sites.
- (2) Does migration among wastelands play a role in maintaining floristic diversity? To address this, we compared matrices of floristic distances to matrices of geographic distances between wasteland sites.
- (3) Do urban structures surrounding wasteland sites impact floristic diversity? To address this, we studied the relationship between the floristic diversity of wasteland sites and the presence of various urban structures around the sites, as inferred from the Land Use Pattern.

## MATERIAL AND METHODS

### Study Area

Wasteland floristic diversity was studied in Hauts-de-Seine (France), a crescent-shaped administrative department (48°50' N; 2°14' E) located in the heart of the Greater Paris area (which represents a total of 2,720 km<sup>2</sup>). This department is composed of 36 boroughs that cover a total area of 176 km<sup>2</sup> (Figure 1). The climate is oceanic with continental trends: the mean annual temperature is 11.7°C with a thermal amplitude of 16°C and an average annual rainfall of 641 mm. The department is located between the Beauce Plateau and the Seine River Valley, comprising of a plain, small hills and a plateau. It is one of the most densely inhabited zones of France, with a human density of 8,118 inhabit./km<sup>2</sup> (INSEE 1999) as opposed to 95 inhabit./km<sup>2</sup> on average in France. The successive Land Use Patterns from 1982 to 2003 were provided by IAURIF (2003). They show, in particular, that built zones have covered about 70% of the territory for more than 20 years (IAURIF 2003, see Figure 1).

### Sampling Design and Inventories

The flora of Hauts-de-Seine was inventoried over all the department, on a total of 986 sites, using a stratified sampling strategy, that is, the surface of inventoried sites in a given habitat was proportional to the total area occupied by this habitat in the department (see Muratet 2006 for details on site location and sampling methods). Each site was inventoried once between 2001 and 2005, in spring, summer or autumn. During an inventory, we recorded all wild vascular plant species over the

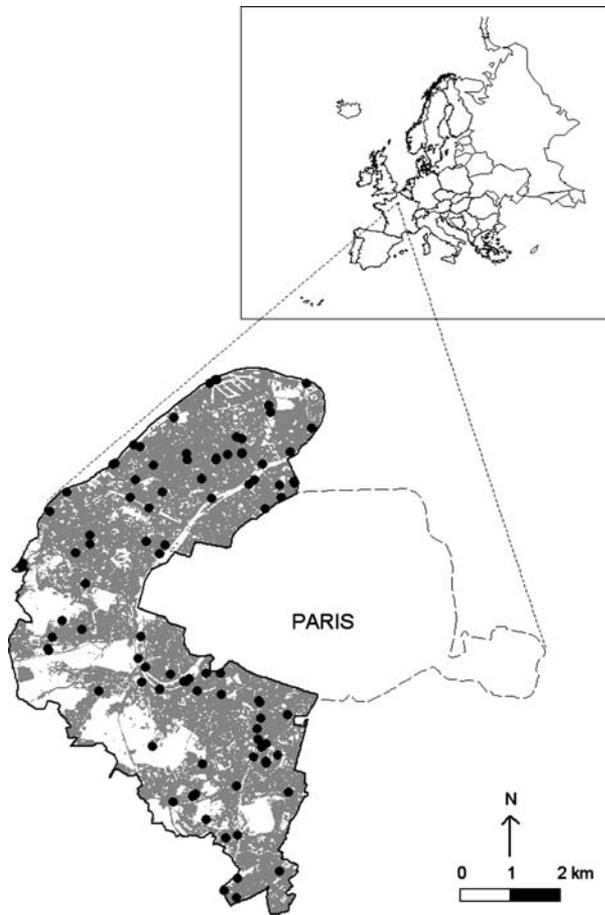


Figure 1. Location of the study area, the French department of Hauts-de-Seine (Built zones are in grey and open zones in white, see [Appendix](#)). Each point corresponds to a studied wasteland site.

whole site area (“global method”), that is, we dismissed cultivated and ornamental species. Species were classified as “indigenous” or “naturalized” according to a list compiled by professional botanists of the National Botanical Conservatory of the Parisian Region (CBNBP). Naturalized species are non-indigenous species that now behave like indigenous species (Richardson and others 2000). Several environmental parameters were also recorded: light exposition, slope, type of parent rock, and site geomorphology.

Among the 986 inventoried sites, 98 were wastelands with areas ranging from 12 to 18,263 m<sup>2</sup>. As mentioned above, wastelands were defined as sites where vegetation management has been more or less temporarily abandoned. In cities, four types of wastelands can be found (1) Wastelands located in building sites and vacant urban areas, corresponding to transitions in land use, (2) Wastelands located in open urban areas, corresponding to irregularly managed plots of gardens,

(3) Wastelands located in built-up areas (dwellings, activities, facilities), corresponding to abandoned industrial plots or to small unused interstices in the built matrix, (4) Wastelands located in subnatural environments (for example, woods or river banks), corresponding to the disturbed edges of natural zones.

In 13 of these sites, chosen for their accessibility, an alternative method of inventory (“quadrat method”) was used in addition to the “global” method to test the accuracy of the latter at producing unbiased estimates of local plant diversity. In the quadrat method, we performed five replicate inventories within each site, using 3 m × 3 m quadrats that were placed systematically in the field to avoid an observer bias during the choice of quadrat location. We used the CAPTURE program in the Mark software (Rexstad and Burnham 1991) to obtain species richness estimates. The model including heterogeneity effect on species detectability only,  $M(h)$ , yielded the best fit of data and was retained to analyze the “quadrat method”. We found no significant difference between the richness observed via the “global” method and the richness estimated by capture-recapture via the “quadrat” method (Wilcoxon signed-rank test,  $P = 0.097$ ) although observed richness was generally lower than estimated richness. Therefore, the global method seems to provide an accurate and confidently unbiased measure of species richness, and the results we present in the following are derived from this method only.

## Geographic Information System

We mapped the distribution of wastelands in Hauts-de-Seine (Figure 1) and calculated their area using a Geographic Information System (MapInfo software, MapInfo Corporation 2004). Additional information regarding wastelands was retrieved from six updates of the Land Use Pattern (LUP), performed in 1982, 1987, 1990, 1994, 1999, and 2003 and provided by IAURIF (2003).

The LUP contains 83 different classes that were grouped into nine major classes for this study ([Appendix](#)). We identified the LUP classes in which wastelands were found. By comparing the different updates of the LUP (Table 1), we could estimate the age of each wasteland site, defined as the number of years during which the site LUP class remained the same. We also identified the LUP classes around each wasteland, to characterize their urban environment.

**Table 1.** Age Classes inferred from the Land Use Pattern (LUP) Updates

| Age classes (years) | Lup conditions                          | Number of wastelands | Mean area (m <sup>2</sup> ) |
|---------------------|---|----------------------|-----------------------------|
| Younger than 4      | In the same LUP class since 2003        | 10                   | 2,027(BC)                   |
| Between 4 and 13    | In the same LUP class from 1994 to 1999 | 15                   | 4,053 (AB)                  |
| Between 13 and 21   | In the same LUP class from 1987 to 1990 | 5                    | 6,743 (A)                   |
| Older than 21       | In the same LUP class since 1982        | 58                   | 1,261 (C)                   |

Significant differences in area ( $P \leq 0.05$ , Tukey's test) are indicated by different letters. Two groupings were performed so that each age class contained at least five inventories. Age could be inferred for 88 of 98 sites only, because LUP type was not available for 10 wasteland sites.

## Data Analysis

**Indices of Floristic Interest.** To study the impact of the urban environment on the floristic interest of wastelands, we used three parameters of floristic interest for a given site: (1) species richness (Rich), the total number of species observed in the site, (2) indigeneity (Ind), the proportion of indigenous (versus naturalized) species and (3) rarity (Rar). For a given species, rarity (Rar<sub>sp</sub>) is the fraction of sites (including all habitats) in the department in which the species was not observed. Rar<sub>sp</sub> varies between 0 (the species was observed in all sites) and 985/986 (the species was observed in a single site in the department). At the site level, rarity (Rar) is the mean of specific rarity indices over all species observed in the site.

**Relationship Among Floristic, Environmental and Geographic Distances.** As site area has a major influence on species richness (see Results), sites were grouped into four quartile area classes to avoid confounding area effects when analyzing the effect of geographic and environmental distances. The geographic distance between two sites was defined as the Euclidean distance between their barycentres. The floristic distance between two sites,  $d_f$ , measuring the difference in species composition, was calculated from the global inventory data via the Jaccard similarity index  $s_f$  with the R software (R Development Core Team 2005), using the ADE4 package (Thioulouse and others 1997) as follows:

$$d_f = \sqrt{1 - s_f} \quad (1)$$

where  $s_f$ , the fraction of total species found in both sites. The environmental distance between two sites was calculated via the Gower index  $s_e$ , which includes a correction factor for the missing values, using the ADE4 package (Thioulouse and others 1997).

$s_e$  = number of environmental parameters with identical values in both sites/(total number of values for all parameters + number of parameters values not found in both sites).

Correlations between floristic distance and geographic or environmental distances were tested with simple and partial Mantel tests based on Pearson correlations using the *vegan* package from the R software (Oksanen and others 2005).

**Impact of Urban Environment on Floristic Interest.** We analyzed the variation of floristic interest indices using three ANCOVAs where site richness, indigeneity or rarity was a function of (1) the LUP class in which sites were located, (2) distance from the center of Paris, a good proxy for urbanization intensity (the proportion of built-up areas strongly depends on the distance to the center of Paris, linear regression,  $proportion = 1.18 - 0.05 \times distance$ ,  $r^2 = 0.83$ ,  $P < 0.0001$ ), (3) site age, (4) season of inventory, (5) all pairwise interactions among these four variables, and (6) simple effects of ecological parameters: parent rock, geomorphology, slope, and exposition. Site area was added as a quantitative covariate in the model. Using a stepwise AIC method, this full model was simplified to retain the most informative model.

We assessed the impact of urbanization patterns around wastelands on their floristic interest by studying the relationships between (1) floristic interest indices (Rich, Ind and Rar) of a wasteland site and (2) variables with a significant effect retained from the ANCOVA above, plus the proportion of area occupied by the 9 LUP classes within a 200 m buffer around the site center. The LUP class area proportions were obtained using the MapInfo software (MapInfo Corporation 2004) and Arcsin-root transformed to approach normality. The 200 m radius was identified in a former study as the best radius fitting floristic variation in Hauts-de-Seine to the proportion of the different LUP classes (Muratet 2006). Hierarchical partitioning (Walsh and McNally 2004) was conducted on  $r^2$

values to isolate parameters with a significant independent effect on the site floristic interest and to correct for multicollinearity (McNally 2002). A randomization (500 times) permitted the segregation of the significant independent effects on the Rich, Ind and Rar indices.

## RESULTS

### Description of Studied Wastelands

The 98 studied wastelands were distributed over the whole area of the Hauts-de-Seine department (Figure 1) and were observed in each of the nine LUP classes (Figure 2). However, they were more frequently located in the “building and vacant area” (BUILVAC) class (28%), corresponding to transitions in land use yielding temporary abandoned plots and in the “open and rural areas” (OPENRUR) class (25%), that is, irregularly managed plots of horticulture, orchards, gardens, parks, golf courses and sport fields. Wastelands in the built (ACTI, COLL, FACI, INDI and TRAN) classes corresponded to abandoned industrial plots or to small-unused interstices in the built matrix. There were very few wastelands in natural environments (WATE and WOOD) (2%).

In contrast to what we expected for frequently disturbed habitats, wastelands were generally old, with 66% of sites older than 21 years. The oldest (>21 years) wastelands were significantly smaller than sites of intermediate age (between 4 and 21 years) ( $r^2 = 0.21$ ,  $P = 0.0002$ , Table 1).

### Floristic Results

We recorded a total of 365 vascular plant species in the Hauts-de-Seine wastelands, which corresponds to 58% of the total species richness recorded over the whole department. The mean richness was 39 species per site, varying between 5 and 92 species.

Among the 365 species, nine were found in more than half of the sites (*Artemisia vulgaris* L., *Cirsium arvense* (L.) Scop., *Plantago lanceolata* L., *Picris hieracioides* L., *Urtica dioica* L., *Taraxacum campyloides* G.E.Haglund, *Calystegia sepium* (L.) R.Br., *Rumex obtusifolius* L., and *Buddleja davidii* Franch.). All are very common species that are also frequently found in other habitats of the study area. These species are perennial species that prefer the nutrient rich soils generally found in urban zones.

A total of 109 species among 365 were observed only once in wastelands but none of them is protected. These species could be rare species at the department scale (for example, *Lythrum hyss-*

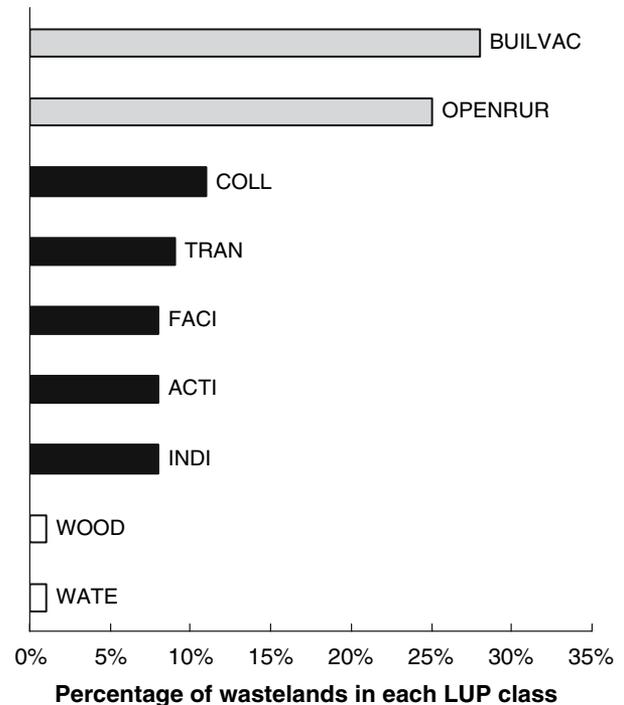


Figure 2. Percentage of wastelands in each LUP type. Open urban areas are in grey, natural areas in white and built zones in black. Percentages were calculated over 88 sites only, because the LUP type was not available for 10 sites.

*opifolia* L., *Euphorbia cyparissias* L., and *Verbascum lychnitis* L., which were observed in two sites only over the entire department) or not adapted to wasteland habitat (for example, *Ranunculus ficaria* L., *Veronica hederifolia* L., and *Carpinus betulus* L., which were found in numerous sites (>100) in non-wasteland habitats). In fact, only four species observed in wastelands are considered endangered at a regional scale (*Cardamine impatiens* L.) or of floristic interest in the region (*Nepeta cataria* L., *Chondrilla juncea* L., and *Torilis nodosa* (L.) Gaertn.) (CSRPN and DIREN Idf 2002), but all four were observed in at least three sites (up to 10 sites for *Torilis nodosa*).

Finally, 73 (20%) observed species were naturalized species. Within sites, the fraction of naturalized species varied between 0 and 46%, with a mean of 15%. This proportion was not significantly dependent on wasteland age ( $r^2 = 0.009$ ,  $P = 0.86$ ). Each naturalized species remained somewhat rare, being found on average at 7.5 of the 98 sites (vs. 11.3 for indigenous species); in addition, 27 of the 73 naturalized species were found in a single site. However, a number of naturalized species that are considered invasive by managers of green spaces

were also found in a large number of wasteland sites. Five of the main invasive species in the Greater Paris area, namely *Buddleja davidii* Franch., *Solidago canadensis* L., *Ailanthus altissima* (Mill.) Swingle, *Robinia pseudoacacia* L., and *Reynoutria japonica* Houtt. occurred, respectively in 49, 21, 20, 20 and 18 of the 98 sites we inventoried. *Senecio inaequidens* DC., which is also considered invasive, had a lower occurrence (6/98), but was found almost exclusively in wastelands.

### Relationship Between Floristic, Environmental, and Geographic Distances

Regardless of site area, floristic distances were never significantly correlated with environmental distances (results not shown). In contrast, in the largest sites only (>2,500 m<sup>2</sup>), floristic similarity among sites was significantly negatively correlated with geographic distance (Mantel statistics  $r = 0.214$ ,  $P < 0.001$ , Figure 3); this remained true when the environmental distances among sites were accounted for (Mantel statistics  $r = 0.182$ ,  $P = 0.003$ ).

### Impact of Urban Structures on Floristic Interest

We examined the relationship between (1) the floristic interest of sites (Rich, Ind and Rar) and (2) the significant variables of the ANCOVA and the proportion of each urbanization class within a radius of 200 m around the sites. The results of the hierarchical partition are given Table 2.

**Species Richness.** Site species richness depended exclusively on site area and age: large wastelands or wastelands of intermediate age (4–13 years) had a higher richness than small or old (>21 years) wastelands (Figure 4 and 5).

**Rarity.** Site rarity was influenced by season of inventory (rarity was highest in summer during which most of the plants flower, thus their detectability is at the maximum) and Land Use Pattern in the site (for example, rarer species on average in “open zones” than in “built zones” wastelands, Appendix). The presence of collective or individual dwellings within a radius of 200 m around a site had a significant negative independent effect on species rarity. Inversely, the presence of water (WATE) within 200 m was significantly positively correlated with higher species rarity.

**Indigeneity.** The indigeneity of a site depended on its distance from the center of Paris, with higher indigeneity away from Paris. In contrast to rarity,

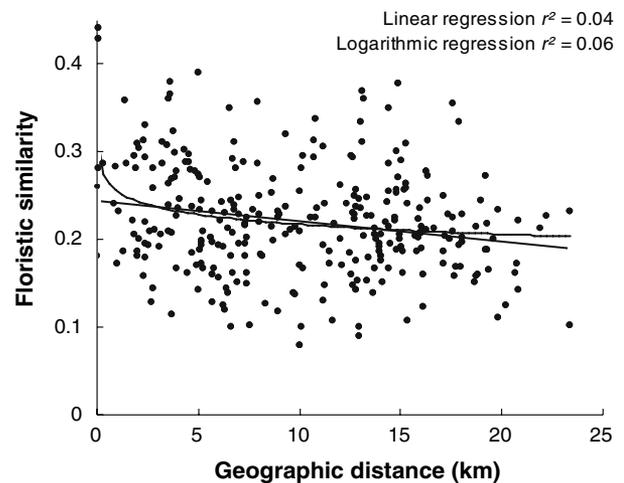


Figure 3. Floristic similarity (Jaccard index = fraction of total species found in both sites) between large sites (>2,580 m<sup>2</sup>) as a function of geographic distance between sites.

the presence of individual dwellings (INDI) within 200 m of a site was positively correlated with the proportion of indigenous species.

## DISCUSSION

We studied 98 wastelands sites in the Hauts-de-Seine department, one of the most densely populated areas in France, to document the significance of wastelands as reservoirs of floristic diversity in urban zones and to explore the factors controlling the diversity of wastelands. In the following, we review the main characteristics of wasteland floristic interest in Hauts-de-Seine and discuss the possible mechanisms underlying the observed patterns as well as the potential role of wastelands in the conservation of urban biodiversity.

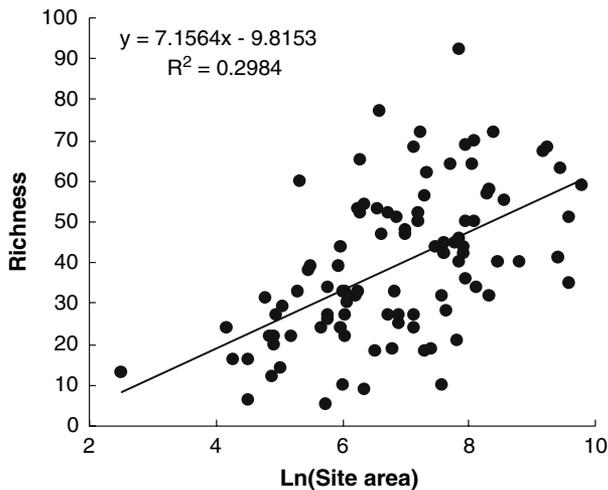
### Characteristics of Plant Communities in Urban Wastelands

Wastelands seem to be a relatively rich habitat of urban zones: their floristic richness represents 58% of the total richness observed in the whole study area, which makes wastelands the richest habitat in the department (365 species among the 626 species recorded), followed by urban lawns (303 species) (Muratet 2006). This value is somewhat similar to that observed in a comparable study in Düsseldorf, where wasteland richness represented 51% of the total richness (277 among 550 species recorded in the whole city, Gödde and others 1995). Despite high species richness, a substantial fraction of the observed species consisted of naturalized species

**Table 2.** Results of a Hierarchical Partition on  $r^2$  for Independent Contributions from 500 Randomizations of Data Matrices for Potential Explanation of the Floristic Interest of Sites (Rich, Ind and Rar)

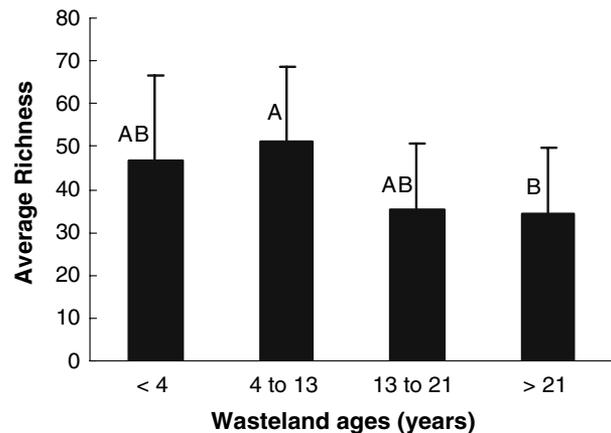
| Predictor variables   | $r^2$ values |           |             |
|---|--------------|-----------|-------------|
|   | Richness     | Rarity    | Indigeneity |
| Area  | 0.045*, +    | 0.015     |             |
| Age   | 0.054*       |           |             |
| Season  |              | 0.025*    |             |
| LUP type  |              | 0.034*    |             |
| Distance to the center of Paris                               |              |           | 0.027*, +   |
| Activities (Warehouses, Offices, Companies)                   | 0.006        | 0.007     | 0.004       |
| Building sites and Vacant urban                               | 0.007        | 0.010     | 0.001       |
| Collective dwelling   | 0.006        | 0.021*, - | 0.011       |
| Facilities (Education, Health, Administration, Cemeteries...) | 0.004        | 0.009     | 0.004       |
| Individual dwelling   | 0.011        | 0.029*, - | 0.022*, +   |
| Transport (Railways, Highways, Parking lots)                  | 0.003        | 0.008     | 0.015       |
| Water   | 0.005        | 0.052*, + | 0.012       |
| Woods and forests   | 0.009        | 0.008     | 0.016       |
| Open urban and rural areas                                    | 0.013        | 0.013     | 0.016       |

Stars indicate significant contribution at the upper 95% confidence limit, the plus (respectively minus) sign indicates a positive (respectively negative) relationship. The explanatory variables include the significant variables of the ANCOVA for each floristic interest parameter, plus the proportion of each urbanization class (Appendix) within a radius of 200 meters around the sites.

**Figure 4.** Relationship between site richness and site area.

(20%), which is more than the department average of 17% (Student's  $t$  test =  $-2.75$ ,  $P$ -value =  $0.006$ ). This may have important consequences in terms of conservation policies.

A large number of species observed in a majority of the wastelands were generally temperate, almost cosmopolitan species: *Artemisia vulgaris* L. (found in 81% of the sites), *Cirsium arvense* (L.) Scop. (72%), *Plantago lanceolata* L. (65%), *Picris hieracioides* L.

**Figure 5.** Average richness as a function of wasteland age. Error bars indicate standard deviations. Significant differences ( $P \leq 0.05$ , Tukey's test) are indicated by different letters.

(63%), *Urtica dioica* L. (59%), *Taraxacum campylodes* G.E. Haglund (52%), *Calystegia sepium* (L.) R.Br. (51%), *Rumex obtusifolius* L. (50%), and *Buddleja davidii* Franch. (50%). These species are characterized by (1) perenniality, (2) high dispersal capacity and seed production, and (3) high nitrophily (average N Ellenberg index of 7, Ellenberg 1979). *Cirsium arvense*, *Rumex obtusifolius* and *Buddleja davidii* have also been mentioned by Godefroid and others (2006) among the most frequent species

of wastelands in Brussels. On average, species that are considered invasive by managers were more frequent in wastelands habitat (for example, 76% of sites harbored at least one of the six main invasive species (*B. davidii*, *S. canadensis*, *A. altissima*, *R. pseudoacacia*, *R. japonica*, and *S. inaequidens*) than in most other habitats of Hauts-de-Seine (on average 35% of other sites were "invaded"). Wastelands have a similar level of invasibility than other highly disturbed habitats (that is, edges of running water (65%), wet thickets (74%) or railway slopes (78%)) and could, similarly, play a major role in invasion processes.

Wastelands also exhibited a large number of locally very rare species (17), that is, species that were observed only once in the department. These species, because they are locally very rare and occupy temporary habitats, owe their maintenance through time to the ability to migrate among sites. Their maintenance in the department relies on the existence of networks of wastelands, that is, groups of geographically close wastelands that are connected through the existence of urban structures enabling gene flow (streets, parks, river banks...). In the wastelands of Hauts-de-Seine, we observed a single regionally protected species. The presence of such a rare species was unexpected because protected species generally grow in rare or declining habitats (such as marshes, calcareous lawns...) and are rarely observed in common, human-made habitats.

### Factors Influencing the Floristic Interest of Wasteland Sites in a Densely Populated Urban Area

**Anthropogenic Parameters.** We defined wastelands as sites where vegetation management had been temporarily abandoned, but not long enough for an identified natural habitat (for example, a forest) to settle. Therefore, a large number of wastelands arise following destruction of buildings (BUILVAC) and are temporarily abandoned until a new project is undertaken. This transition state of wastelands in building and vacant areas makes them highly vulnerable and, in contrast to other wastelands in the department, they are generally rather young because of the rapid turn over of such habitats within cities (70% of wastelands in BUILVAC were younger than 13 years). Wastelands in building sites and vacant areas were also the largest wasteland types (4,494 m<sup>2</sup> on average).

A significant number of wasteland sites, ranging from 12 to 18,260 m<sup>2</sup>, have also been observed in other classes of the land use pattern. Wastelands

observed in open urban and rural areas (OPEN-RUR) corresponded to green spaces that were less regularly managed than lawns. They were older on average than sites in building and vacant areas (44% older than 21 years) and their floristic diversity was more likely to depend strongly on the intensity of management. Wasteland sites observed in the different types of built urban areas (activities, individual and collective dwellings, facilities, transports) corresponded to abandoned industrial plots or to small interstices in the built matrix on which no urban projects were developed. These sites were significantly the smallest ones (808 m<sup>2</sup> on average) and were highly isolated (because they were surrounded by construction), but they were stable in the long term (92% were older than 21 years). Finally, old wastelands (all older than 21 years) could also be observed in natural plots (water and wood), but they represented a minor fraction (2%) of wasteland sites. These wastelands were observed in the disturbed edge of natural zones.

Site age and area, which can be considered anthropogenic parameters because they are predominantly controlled by urban management, had a significant impact on the biodiversity of wastelands. The largest sites were also the richest ones (Figure 4), as found in similar studies (Davis and Glick 1978) and may be more resistant to potential disturbance than small sites (Grumbine 1990). We also found a non-monotonous relationship between site age and richness, with maximum floristic richness observed in sites of intermediate age (4–13 years, Figure 5). Old wastelands were significantly less diverse than sites of intermediate age. This observed maximum richness at intermediate age could be attributable to classical patterns of ecological succession, with transient high levels of diversity but establishment of a smaller number of species in the stable communities resulting from the initial colonization/competition processes (Horn 1974). Alternatively, as most (70%) old wastelands were situated in built urban areas, the urban matrix may isolate them from each other, thus preventing exchanges of species (via seeds for example) and resulting in lower levels of floristic diversity.

The proportion of indigenous species was found to be positively correlated with the distance from the center of Paris, a correlate of urbanization intensity. This pattern was already observed in other cities (McDonnell and Pickett 1990; Maurer and others 2000) and highlights the role of major communication routes and perturbations in the establishment of non-native species. The average

percentage of aliens in central European cities is 13.7% higher than their representation in the total species pool available in the region, indicating a remarkable concentration of aliens in urban areas (Pysek 1998). The proportion of non-native species rises from 6% in nature preserves outside the city of Berlin to 25% in the suburbs to 54% in the most intensively urbanized central areas (Kowarik 1995).

**Environmental Parameters.** Unexpectedly, we did not find evidence of any effect of the environmental parameters (parent rock, exposition, slope, or geomorphology) on wasteland floristic interest and, accordingly, the floristic distance among sites was not significantly correlated with their environmental distance. This likely does not reflect an actual absence of environmental effects in urban areas, as these are unavoidable and have been observed by Godefroid and others (2006) in Brussels, but may rather be due to limited accuracy of measurements or lack of statistical power. For example, the use of parent rock (not retained in the final model of ANOVA) to describe site environment might be inefficient because, in urban and industrial areas, the ground is usually covered with alien substrates from other geographical regions (for example, railway ballast, mine spoil), with artificial substrates (for example, slag), or with a mixture of artificial and natural substrates (for example, slag/clay) (Rebele 1994). In addition, site slope and light exposition were very homogeneous across studied wastelands, with more than 75% of sites having a slope less than 1 (that is, no specific exposition). This is the result of strong urbanization, which tends to level all surfaces. Site geomorphology (hill, plain, valley and so on) may not have any effect on floristic interest in sites of such a fragmented landscape and may be relevant only in large natural landscapes. Finally, soil type and especially soil fertilization frequently have a conspicuous role in floristic composition and diversity in urban context (Peet and others 1983). However, this parameter was so heterogeneous within a site that a much larger number of samples would have been required to adequately explore its influence.

**Isolation by Distance, Migration Among Wasteland and Non-wasteland Sites.** In large sites, we detected significant isolation by distance for floristic diversity, that is, large neighboring sites were often floristically more similar than distant sites. This, together with the observed absence of environmental effects on floristic interest, suggests that migration of species among large sites might have a significant impact on local floristic composition,

which is influenced by the pool of available species in the neighborhood and their capacity to disperse/colonize. In contrast, small sites, which have a lower probability of receiving propagules by chance and are often isolated by the matrix of buildings, are less influenced by the composition or surrounding sites.

The supply of species from non-wasteland sites likely influenced floristic interest in wastelands as well. We have shown that the presence of water (rivers and ponds notably) within a radius of 200 m had a positive impact on the floristic rarity of a wasteland. Humid habitats are generally highly diverse and harbor many rare species of high conservation interest. In wastelands situated near water sites, we found *Alnus incana* (L.) Moench (that was observed in only four sites in the department (986 Sites), *Alopecurus pratensis* Mattf. (four sites), *Cardamine impatiens* L. (four sites), *Equisetum telmateia* Ehrh. (three sites) and *Stachys palustris* L. (five sites).

In contrast, the presence of collective and individual dwellings around a site had a significant negative influence on floristic rarity. These findings have major consequences for management plans. They indicate, for example, that the establishment of dwelling districts will certainly reduce the quality of neighboring wastelands and more generally of green lands. However, the presence of individual dwellings seemed to have a positive impact on the proportion of indigenous species in the wastelands around. This result is somewhat surprising, as small gardens surrounding houses were expected to host many exotic species for ornamental purpose. It may be that these cultivated exotic species remain "trapped" in the gardens, and that meticulous gardening practices prevent the dispersal and establishment of exotic species considered as weeds (for example, *Conyza canadensis* and *C. sumatrensis*, *Artemisia annua* ...).

## CONCLUSIONS

Our study confirms that urban wastelands are a habitat of crucial importance in urban areas. Thanks to their large and homogeneous distribution in the department, they host a substantial proportion of floristic diversity of cities and certainly play a key role in favoring exchanges among urban habitats. Thus, although the preservation of wastelands has little consequence for the conservation of rare species in the present case, our study shows that their maintenance is necessary to protect urban biodiversity as a whole because they

favor connectivity among sites and provide a source of species to colonize vacant sites. Unfortunately, wastelands are one of the more threatened urban habitats due to urban intensification: for example, the total surface of building and vacant areas, which contain a large number of wastelands (Figure 2), has decreased by 24% in the last 20 years in Hauts-de-Seine.

In this work, we could not study whether the presence of wastelands has a positive impact on the floristic diversity of other habitats in the department because we did not locate all wastelands and could not correlate the diversity at a given site with the presence/absence of wastelands in the neighborhood. However, we have shown that humid zones have a positive impact on the mean species rarity of wastelands, and it is highly likely that, in a symmetrical way, wastelands are beneficial to other habitats. Assessing the actual impact of wasteland sites on the floristic diversity of other urban habitats will require further investigation; nonetheless our results suggest a number of simple actions that could be taken to favor the preservation of the floristic diversity in the Hauts-de-Seine. For example, the maintenance and the creation of large sites (>2,500 m<sup>2</sup>) could favor species exchange among wastelands, lower the extinction risk of plant populations and provide seeds to colonize new sites. Note however that invasive species were frequently found in wastelands, so highly connected sites could also act as relays to favor the spread of these species. The role of wastelands, a habitat submitted to frequent disturbance, in species invasion remains unclear. Additional information regarding abundance within sites is required to understand the dynamics of invasive species in these habitats. Finally, we also suggest that too rapid turnover should be avoided: waiting about ten years before construction of new buildings would leave enough time for installation of highly diverse plant communities and for a maximum contribution to the floristic diversity of surrounding sites.

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#### APPENDIX: ABBREVIATIONS FOR LAND USE PATTERN CLASSES (IAURIF 2003)

|                    | Land use patterns | Definitions   |
|--------------------|-------------------|---|
| <b>Built zones</b> | ACTI              | Activities (Warehouses, Offices, Companies)   |
|                    | COLL              | Collective dwelling   |
|                    | FACI              | Facilities (Education, Health, Administration, Cemeteries, Electricity, Gas, Petroleum)   |
|                    | INDI              | Individual dwelling   |
|                    | TRAN              | Transport (Railways, Highways, Parking lots)  |
|                    | BUILVAC           | Building sites and vacant urban   |
| <b>Open zones</b>  | OPENRUR           | Open urban areas (Parks, Gardens, Sports, Camping, Golf, Hippodrome) and rural (Truck farmings, horticulture, orchards, breeding grounds, grounds and pits) |
|                    | WATE              | Water   |
|                    | WOOD              | Woods and forests   |
|                    |                   |   |

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