Landscape dynamics and habitat selection by the alien invasive *Fallopia* (Polygonaceae) in Belgium

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Abstract

Habitat patch colonization dynamics and distribution patterns were analysed at a landscape scale in four invasive *Fallopia* (Polygonaceae) species. *Fallopia sachalinensis* and *F. aubertii* were uncommon and population expansion was not evident during the three consecutive years of study. The two most widespread species, *F. japonica* and *F. × bohemica* displayed similar habitat selection patterns with ruderal and natural/semi-natural forests favoured. The highest densities of *F. japonica* and *F. × bohemica* individuals were at the edge of preferred habitat patches with different patterns of edge selection. Linear network played an important role in species invasion, with 71% of all *F. japonica* and *F. × bohemica* occurring within a 10 m buffer of total linear networks (roads, railways, and rivers). However, the buffer represented only 14.5% of the total landscape surface. The rate of population increase was higher for *F. japonica* (75.8% and 35.2%, in 2002 and 2003, respectively) than for *F. × bohemica* (63.6% and 0% in 2002 and 2003, respectively) and was largely the result of intra-patch dynamics with low inter-patch colonization. The total surface area occupied by *Fallopia* clones in the landscape grew by 34.7% over 2 years of the study, with comparable area growth means for *F. japonica* and *F. × bohemica* (34.9% and 34.7%, respectively). The hypothesis that *F. × bohemica* exhibits higher invasive dynamics due to both clonal and sexual reproduction was not supported by our results.

Keywords : *Fallopia* ; Habitat selection ; Hybridization ; Invasive plants ; Landscape ; Population dynamics

INTRODUCTION

Alien species invasions are considered one of the most severe threats to global biodiversity (Vitousek et al. 1997; Wilcove 1998). Invasive species distributions across a landscape result from interactive processes including colonization, competition, extinction and evolution (Huang and Zhang 2007). Analysing the distribution patterns of alien invasive species at a landscape scale is key to establish management priorities for invasion control and habitat protection (Hobbs and Humphries 1995; Collingham et al. 2000; Marvier et al. 2004).

Most research on alien invasive species distributions has focused on the rates of expansion on large-scales (Conolly 1977; Perrins et al. 1993; Godefroid 1996). In addition, ecosystem invasibility has been investigated (Lonsdale 1999; Pyšek and Richardson 2006) but analyses were often conducted at spatial scales too large to provide adequate data on landscape scale habitat selection and the dynamics of habitat patch colonization (Collingham et al. 2000; Wang and Wang 2006; Adriaens et al. 2008) (but see Bímová et al. 2004). The application of habitat selection indices provides a quantitative measure of the relative use of habitats in proportion to their availability (Cock 1978; Buse 1988; Manly et al. 1993; Kamler and Gipson 2000; Duriez et al. 2005; Zimmer and Power 2006).

At a landscape scale, another aspect of invasive species distributions addresses invasion mechanisms along linear networks (communication routes and habitat borders). Communication routes (rivers, roads, and railways) and adjacent vegetation strips are recognized as human disturbance factors substantially affecting the natural landscape (Forman and Alexander 1998; Martinez and Wool 2006). River bank management, and road and rail construction cause considerable alterations to natural communities, such as clearing soil and natural vegetation, increasing light at ground level and modifying drainage (Christen and Matlack 2006; Richardson et al. 2007). Communities subjected to disturbance regimes are dominated by disturbance-tolerant species and are particularly vulnerable to invasion by alien species, which are often well adapted to disrupted environments (Fox and Fox 1986; Panetta and Hopkins 1991; Forman and Alexander 1998; Parendes and Jones 2000; Song et al. 2005). Linear networks may also act as vehicles for subsequent migration into adjacent habitats (Pyšek and Prach 1993; Christen and Matlack 2006; Richardson et al. 2007).

In the current study, we explored habitat selection and spread dynamics of four clonal alien invasive plant species at a landscape scale in the genus *Fallopia* Adans. (Polygonaceae), including *F. japonica* (Houtt.) Ronse Decraene, *F. sachalinensis* (F. Schmidt Petrop.) Ronse Decraene, *F. × bohemica* (Chrtek et Chrtková) J. P. Bailey, a proposed hybrid between *F. japonica* and *F. sachalinensis,* and the climbing perennial *F. aubertii* (L. Henry) Holub (Syn. *F. baldschuanica* (Regel) Holub). Species comprising the genus *Fallopia* originated in Asia and are considered among the most troublesome alien invasive species in Europe and Northern America (Weber 2003). *Fallopia japonica* and *F. sachalinensis* were introduced to Belgium and its neighbouring countries at the end of the ninetieth century as ornamental species and/or fodder. More recently, *F. aubertii* was also introduced as an ornamental species (Vanden Berghem 1997; Verloove 2002; Saintenoy-Simon 2003). The status of *F. × bohemica* is still discussed as it is not clear whether the hybrid was produced in situ or was also introduced independently of the parental species (Tiébré et al. 2007b). At the beginning of the twentieth century, plants remained uncommon until 1945, when various accidental introductions into natural habitats resulted in species expansion (Godefroid 1996; Vanden Berghem 1997). *Fallopia* taxa are now widely naturalized and some are a threat to native ecosystems. Invasive alien *Fallopia* are extremely difficult to control by both manual and chemical methods. The combination of successful vegetative propagation (Bímová et al. 2003; Pashley et al. 2007), high competitive capacity (Mandák et al. 2004), hybridization and polyploidization (Tiébré et al. 2007a) and sexual reproduction (Child and Wade 2000; Hathaway 2000; Tiébré et al. 2007b) certainly contribute to the success of these invasive plants.

Vegetative regeneration has been recognized as the primary mode of reproduction in *Fallopia* outside their native range (Beerling et al. 1994; Child and Wade 2000; Weber 2003). This was due to the male sterility of the most widespread taxa *F. japonica.* However, multiple interspecific hybridizations and polyploid formation have been described among the species (Bailey and Stace 1992; Bailey 2003; Mandák et al. 2004; Tiébré et al. 2007a, b), demonstrating the presence of sexual reproduction within the species complex. *Fallopia × bohemica* is a presumed hybrid between *F. japonica* and *F. sachalinensis.* Hybridization has served to increase the genetic variability in *F. × bohemica* compared to the parental species, and enhance propagule pressure via the production of viable hybrid seed and effective seed dispersal mechanisms. In addition, *F. × bohemica* grows and spreads faster compared to its progenitor species (Bímová et al. 2003; Mandák et al. 2004). The differences in genotypic diversity, reproductive success and regeneration characteristics in *F. × bohemica* may induce different invasion rates and distribution dynamics at the landscape scale compared with other *Fallopia* species. Hybridization is also frequent between *F. aubertii* and other introduced *Fallopia* taxa (Tiébré et al. 2007b), but the resulting hybrids do not establish in the nature (Tiébré et al 2007b).

The spatial distribution of *Fallopia* was mapped on both a continent (Europe) (Jalas and Suominen 1979; Bailey and Wisskirchen 2006) and country scale, the latter also addressing the rates of species expansion (Conolly 1977; Mandák et al. 2004). As a result, an increase in data resolution with decreasing spatial extent was achieved (Collingham et al. 2000). Further studies attempted to identify invaded habitats in the British Isles (Beerling 1991; Beerling et al. 1994; Bailey et al. 1996; Child and de Waal 1997; Hathaway 2000), the Czech Republic (Pyšek and Prach 1993; Mandák et al. 2004), and France (Jager 1994; Boyer 2002; Voinot et al. 2002), but these analyses were largely descriptive. Few studies have evaluated habitat selection at a landscape scale by invasive *Fallopia* species (see for example (Bímová et al. 2004)) or the dynamics of habitat patch colonization by invasive *Fallopia* and the hybrid *F. × bohemica.*

The focus of our study was to analyse the distribution and dynamics of four alien invasive *Fallopia* taxa at a landscape scale with the aim to test two specific hypotheses: (1) *Fallopia* taxa preferentially colonize human-disturbed habitats; (2) Sexual reproduction plays a significant role in *Fallopia* population dynamics resulting in a higher rate of colonization in *F. × bohemica* compared to its progenitor species. Therefore, we addressed the following questions: (1) which habitats were most often selected by the target species in Belgium? (2) At a landscape scale, was the dynamics of colonization of new habitat patches different from the dynamics of spread within habitat patches? and (3) Does the hybrid *F. × bohemica* differ in its habitat selection invasion dynamics at the landscape scale relative to the parental species *F. japonica* and *F. sachalinensis?*

MATERIALS AND METHODS

Study area and population survey

This study was conducted on the upper basin of the Orneau River in Gembloux, Belgium (50°33' N; 4°41' E). The locality is a semi-rural landscape of 1,118 ha comprised of agricultural and urban land. We performed a complete landscape survey in September/October 2001, 2002 and 2003 to locate all individuals of *F. japonica, F. sachalinensis, F. × bohemica* and *F. aubertii* using a 1/10,000 topographical map (National Geographical

Institute, Belgium). Due to the high clonality of *Fallopia* spp., distinguishing ramet from genet within a habitat patch was difficult. Our approach was to identify the dynamics of focal points; therefore we arbitrarily determined that two ramets or groups of ramets separated by more than 1 m represented two different individuals. We acknowledge that different ramets may belong to the same clone. However, our study was designed to serve the following two purposes: (1) distinguish between intra-patch dynamics, likely the result of clone extension; and (2) inter-patch dynamics, presumably the result of new clone settlement, whether by vegetative propagation or seed dispersal. Location, taxonomic status, maximum and minimum diameter of each individual were recorded in the field. The area covered by each individual was estimated from its two longest axes. Data were transferred into a land use cover map Top10v-GIS (National Geographical Institute, Belgium) using Arcview (version 3.2, Environmental Systems Research Institute Inc.).

Habitat assessment

The landscape structure (habitat type and spatial configuration) was characterized on the basis of recent land use cover maps (IGN TOP10V-GIS). The TOP10V-GIS database provided different levels of resolution depending on the habitat type. For example, detailed localisation of some building types compared to a general class for cultivated land. We subsequently grouped the different land use types into more general classes with a similar level of resolution, including natural/semi-natural forest (broad-leaved forests with woody undergrowth and mixed forests with broad-leaved trees and conifers), exotic plantation (poplar plantations and coniferous forests), lawn, meadow, orchard, farming, ruderals (ruderal and ruderal scrubby vegetation, brushwood and waste places), urban non-industrial (intensive human use with much of the land covered by buildings such as schools, pleasure gardens, cemeteries and churches), urban industrial (in use and abandoned commercial and industrial buildings, shelters, silos, plant nurseries, greenhouses, and water catchments), marshland, stagnant water, running water, roads, and railways. For convenience, rivers, roads, and railways were referred to collectively as communication routes.

Habitat selection

Habitat selection was assessed each year independently for each taxon using the selection index $Bsurf_i = [(n_i/N)/(S_i/S)]$ (Manly et al. 1993); where n_i is the surface area occupied by all individuals of each taxon in the ith habitat, N the surface area occupied by all individuals of each taxon, S_i the surface area occupied by the ith habitat and, S the total surface area of the delimited landscape. We used surface area instead of the number of individuals because the latter may be a biased estimate of the species importance in a given habitat due to the characteristic clonality of *Fallopia*. If habitat use is random, the expected B_i value will be 1.0 for each habitat type. Significant departures from 1.0 indicate that habitat use is selective. We employed χ^2 analyses to determine if specific habitat types are used more or less than would be expected under random individual distributions. Comparisons of the use of each habitat type to its availability were performed. Analyses were executed using Mini-tab 2006 (version 15.1.0.0, Minitab Inc.). Population size for both *F. sachalinensis* (one individual) and *F. aubertii* (three individuals) was too low to estimate selection indices, so neither taxon was used in statistical analyses.

Preliminary analyses indicated that individuals of *Fallopia* were often distributed at the edge of habitat patches. The conditions at the ecotone are often different from those in the core habitat, therefore each year we also assessed habitat selection along the margins of habitat types for both *F. japonica* and *F. × bohemica* using the following selection index:

$Bedge_i = [(n_i/N)/(P_i/P)]$, where P_i represents the perimeter of the ith habitat, and P the perimeter of all habitat patches within the landscape unit.

In addition, we evaluated *Fallopia japonica* and *F. × bohemica* distribution along the border of communication routes. Five-meter and 10-m buffers were delimited along railways, roads, and rivers, and the percent of individuals distributed within these buffers was recorded on a yearly basis.

Dynamics of *Fallopia* populations

The global dynamics of *Fallopia* spread was estimated by determining individual density per square kilometre for each species and the rate of increase each year was calculated as (density of individuals$_{year\ x}$)/(density of individuals$_{year\ x-1}$) × 100. The emergence rate of new individuals was determined as the ratio of (new individuals$_{year\ x}$)/(individuals$_{year\ x-1}$) × 100 and the extinction rate for each species was estimated by the ratio (extinct individuals$_{year\ x}$)/(individuals $_{year\ x-1}$) × 100. The dynamics of new patch colonization compared to

propagation within occupied patches was evaluated by addressing patch colonization dynamics for each of the different taxa by recording the number of unoccupied patches on year$_{n-1}$ that was colonized on year$_n$.

To characterize *Fallopia* propagation along linear landscape elements, we followed *Fallopia* growth dynamics along a 3 km segment of a busy road connecting Gembloux to Louvain-la-Neuve (Nationale 4, 50°40' N; 4°37' E). Each individual was located and its length measured at four time periods: September 2001, May 2002, July 2003 and August 2003 using a decametre (Stabila, Germany). The growth of each individual was assessed as the ratio of (observed length for a given period—length of the previous period)/length of the previous period.

The mean size differences (surface area or length) of individuals of *F. japonica* and *F.* × *bohemica* between the different periods were compared for each taxon using paired *t*-tests performed with Statistica (version 7.1, Statsoft Inc. 2005).

RESULTS

Habitat selection

The landscape was composed of 2,175 habitat patches with a mean size ± s.d. = 79.8 ± 172.1 ha. The study area was dominated by farming (crops) and urban/ruderal land uses (Fig. 1). Extensive meadows were also represented and constituted an important habitat type. During the study period, significant changes in the landscape structure were not observed but disturbances such as new building developments and soil displacement were recorded.

Three individuals of *Fallopia aubertii* were recorded on boundary walls in urban non-industrial land and a single *F. sachalinensis* individual was found near a greenhouse also in urban non-industrial land. For both taxa, no additional individuals were documented during the study. Consequently, habitat selection and dynamics were not further considered for the two species. Ruderal habitats were preferred by both *F. japonica* and *F.* × *bohemica,* with selection indices ranging from 13.0 to 13.1 and selection indices of 2.5-2.6 for natural/ semi-natural forests. In all cases, selection indices differed significantly from 1.0 (Table 1). A significant selection index was indicated for urban non-industrial habitats in *F.* × *bohemica* but not *F. japonica.* All other habitats were either not colonized by the two species or the proportion of occupation was not significantly different from expectations under random colonization.

Fig. 1 *Landscape composition on the upper basin of the Orneau River in Gembloux, Belgium, 2001-2003*
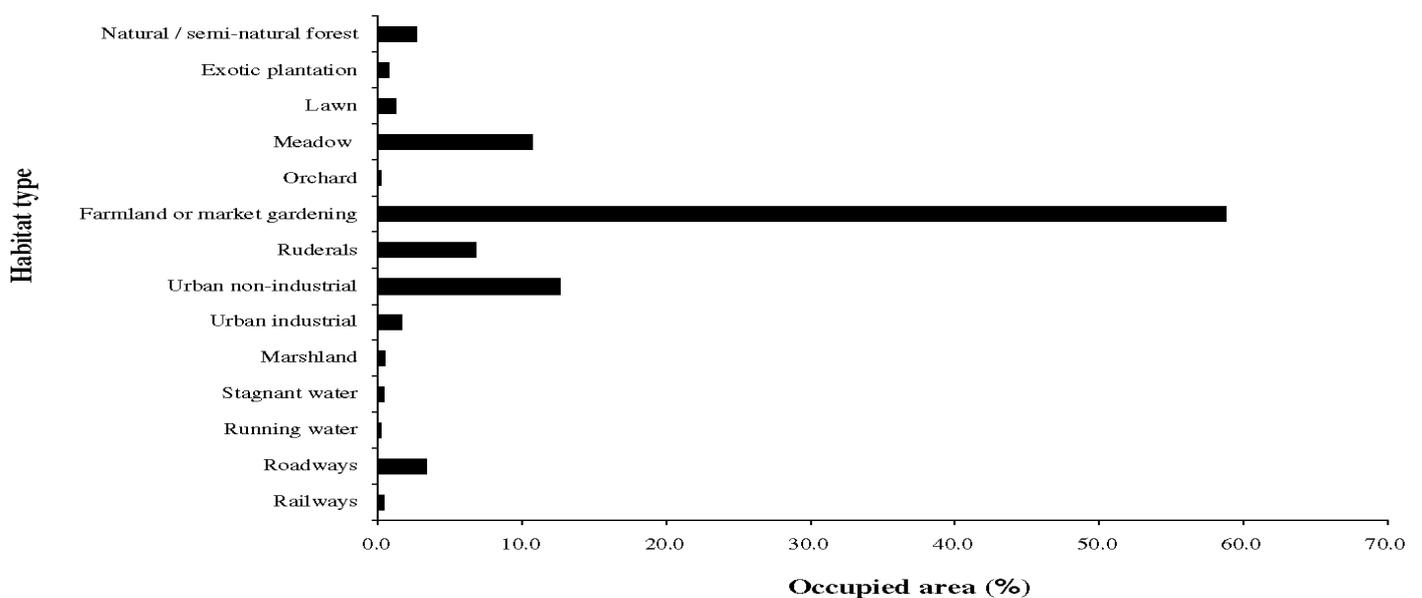
Table 1 *Selection indices (Bsurf_i) for Fallopia japonica and Fallopia x bohemica in different habitat types on the upper basin of the Orneau River in Gembloux, Belgium, 2001-2003*

Habitat type	Both *Fallopia* populations			*Fallopia japonica*			*Fallopia* $\times$ *bohemica*		
	2001	2002	2003	2001	2002	2003	2001	2002	2003
Natural/semi-natural forest	2.6*	2.5*	2.5*	2.7*	2.6*	2.6*	2.4*	2.3*	2.3*
Exotic plantation	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lawn	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Meadow	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Orchard	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Farming	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ruderals	13.0*	13.1*	13.1*	13.4*	13.5*	13.5*	11.6*	11.7*	11.7*
Urban non-industrial	0.4	0.4	0.4	0.1	0.2	0.2	1.2*	1.1*	1.1*
Urban industrial	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Marshland	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Stagnant water	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Running water	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Roadways	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Railways	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Habitats exploited more than expected under random distributions are marked with a asterisk *(P < 0.001)*. For details see the text

Seventy percent of *Fallopia japonica* and 100% of *F.* $\times$ *bohemica* populations were situated along habitat patch borders. Railway borders, running water, and marshland were selected by *F. japonica* and *F.* $\times$ *bohemica* more than expected (Table 2). In all cases, the selection index differed significantly from 1.0. Roadsides and the edge of stagnant water, urban industrial and farmland habitats were favoured by *F. japonica* but not by *F.* $\times$ *bohemica*. *Fallopia* $\times$ *bohemica* exceeded expectations for colonization of meadow margins, exotic plantations, and natural/semi-natural forests edges. Other habitat borders were not selected by either species.

On average, over the 3-year study period, 71% of all *Fallopia* individuals occurred within a 10-m buffer around total linear networks (roads, railways, and rivers) and 59% within a 5-m buffer. However, these buffers represented only 14.5% and 7.9% of the total landscape surface, respectively (Fig. 2). More than half of the individuals were situated along roads.

Table 2 *Selection indices (Bedge_i) for Fallopia japonica and Fallopia* $\times$ *bohemica along different habitat type borders on the upper basin of the Orneau River in Gembloux, Belgium, 2001-2003*

Habitat type	Both *Fallopia* populations			*Fallopia japonica*			*Fallopia* x *bohemica*		
	2001	2002	2003	2001	2002	2003	2001	2002	2003
Natural/semi-natural forest	0.5	0.5	0.5	0.0	0.0	0.0	2.3*	2.3*	2.3*
Exotic plantation	3.4*	3.3*	3.3*	0.9	0.9	0.9	12.5*	12.4*	12.4*
Lawn	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Meadow	0.7	0.6	0.6	0.0	0.0	0.0	3.1*	3.1*	3.1*
Orchard	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Farming	1.0*	1.2*	1.2*	1.3*	1.6*	1.6*	0.0	0.0	0.0
Ruderals	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Urban non-industrial	0.2	0.1	0.1	0.2	0.2	0.2	0.0	0.0	0.0
Urban industrial	1.3*	1.3*	1.3*	1.7*	1.6*	1.6*	0.0	0.0	0.0
Marshland	10.1*	9.8*	9.9*	10.2*	9.8*	9.9*	9.8*	9.7*	9.7*
Stagnant water	1.5*	1.4*	1.4*	1.8*	1.7*	1.7*	0.4	0.4	0.4
Running water	6.7*	6.6*	6.6*	4.7*	4.7*	4.7*	14.1*	13.9*	13.9*
Roadways	1.1*	1.2*	1.2*	1.1*	1.2*	1.2*	1.2	1.2	1.2
Railways	5.3*	5.2*	5.2*	7.0*	6.0*	6.1*	2.0*	1.8*	1.8*

Habitats exploited more than expected under random distributions are marked with a asterisk *(P < 0.001)*. For details see the text

Fig. 2 *Percent Fallopia individuals averaged over 3 years, within 5 and 10-m buffers around rivers, roads and railways on the upper basin of the Orneau River in Gembloux, Belgium, 2001-2003. Percent area covered by these linear networks in the landscape is also depicted*
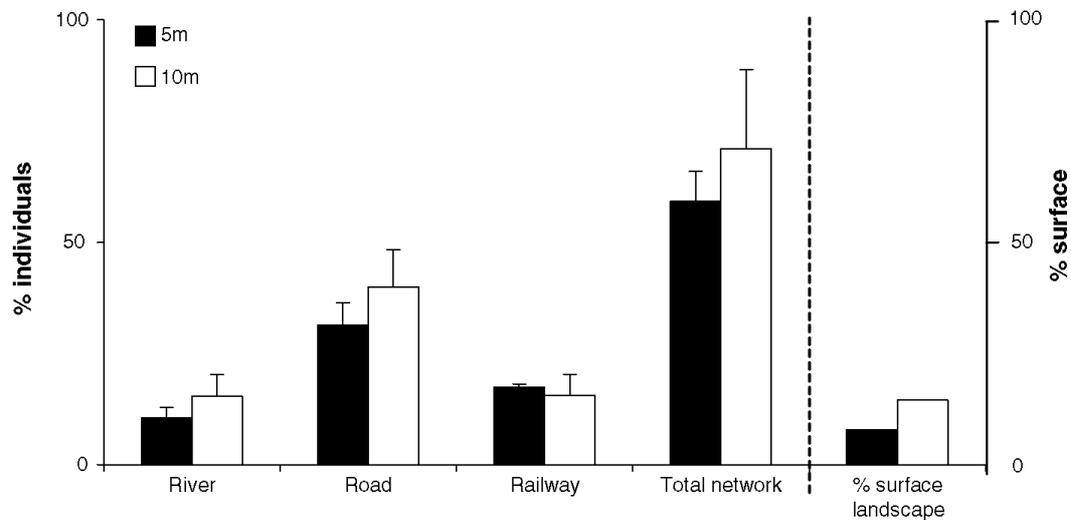
Fallopia population dynamics

A total of 77 *Fallopia* individuals were present in the study area at the onset of the study. *Fallopia japonica* was the most widespread species (80.5% of all individuals, density 5.5 individuals/km^2) (Table 3). *Fallopia* × *bohemica* was less widespread (14.3% of all individuals, density 1.0 individual/km^2). The global spread dynamics *Fallopia* was high but varied between years (rate of increase 68.1% and 26.7% in 2002 and 2003, respectively). The difference resulted from lower emergence rates in 2003 compared to 2002, but in both years emergence rates far exceeded mortality rates (Table 3). The high rate of numerous small individual increases in already colonized patches was in the vicinity of mature plants, and likely the result of vegetative (clonal) reproduction. For both years, the rate of increase in individual numbers was higher for *F. japonica* (75.8% and 35.2%, in 2002 and 2003, respectively) than for *F.* × *bohemica* (63.6% and 0% in 2002 and 2003 respectively). The total landscape surface area occupied by *Fallopia* individuals (represented by *F. japonica* and *F.* × *bohemica)* increased by 34.7%, with comparable area growth increases for *F. japonica* and *F.* × *bohemica* (34.9% and 34.7%, respectively). As much as 39.6% of the individuals covered surfaces greater than 10 m^2, and 24.4% of that number occupied more than 100 m^2. Individual mean surface area decreased over years, but it was due to the emergence of numerous small individuals (<1 m^2). Significant increases in mean size were detected for *F.* × *bohemica* in 2001-2002 (paired *t*-test; dl = 10; *t* = -4.306; *P* = 0.001) but not in 2002-2003 (paired *t*-test; dl = 10; *t* = -2.029; *P* = 0.070). Significant mean size increases were found in *F. japonica* between 2001 and 2002 (paired *t*-test; dl = 57; *t* = -3,293; *P* = 0.002) and 2002-2003 (paired *t*-test; dl = 57; *t* = -3.293; *P* = 0.002).

In contrast to within patch dynamics, the rate of new patch habitat colonization was low. In 2001, *Fallopia japonica* and *F.* × *bohemica* were documented in 38 and 9 habitat patches, respectively (Table 4). In 2002, we recorded a new habitat colonization rate of 4.3% with two habitat patches settled by *F. japonica* (one farmland and one urban non-industrial) and one by *F.* × *bohemica* (one ruderal habitat). In 2003, this rate decreased to 2.1% with three habitat patches colonized by *F. japonica* (two ruderal and one natural/semi-natural forest). The minimal distance between newly colonized and patch occupied the previous year was 10 m and the maximum distance was 105 m.

The growth dynamics analysis identified 31 individuals of *Fallopia japonica* covering 2.3% of the study length along the road connecting Gembloux to Louvain-la-Neuve (Nationale 4) in September 2001. The mean length of individuals was 4.0 ± 4.1 m (mean ± s.d.), ranging from 0.1 to 15.0 m. In May 2002, July 2003, and August 2003 the mean length of individuals increased by 20.1 ± 31.4%, 73.8 ± 256.7%, and 93.8 ± 272.1%, respectively. Three newly established individuals were observed (two in July 2003 and one in August 2003) and two stands merged in July 2003. The two new individuals reported in July 2003 were 3 m from the nearest established stand, and the individual documented in August 2003 was approximately 15 m from its nearest neighbour. Mortality was not observed within any of the patches.

DISCUSSION

Habitat selection in *Fallopia japonica* and *F. × bohemica* was examined employing two complementary approaches: patch scale and patch edge analyses. We used this methodology because a large proportion of *F. japonica* and *F. × bohemica* individuals were distributed at the edge of habitat patches where conditions might be different than in the patch core. The two approaches provided different but complementary data on habitat selection.

Regardless of the approach, *Fallopia japonica* and *F. × bohemica* exhibited a similar pattern of habitat selection. Results of the patch analysis were consistent with our hypothesis that *Fallopia* spp. preferentially colonized disturbed areas, with ruderal habitats most often selected. However, high levels of disturbance seemed to hamper species colonization. Farmland where crop cultivation practices result in yearly soil and vegetation disturbance did not support the species. High levels of perturbation may preclude the establishment of these perennial taxa, but the potential role of herbicide application cannot be excluded. Results drawn from the edge analysis indicated the importance of aquatic and humid habitats in the species distribution patterns. When present, edges of these habitats were favoured.

Analysis of *Fallopia japonica and F. × bohemica* distribution along linear networks showed that in 2001, the majority of individuals (91.0%) occurred within a 10-m buffer along communication routes, which promoted the likelihood of dispersion and expansion to adjacent habitat patches. Growth assessment along the main road between Gembloux and Louvain-La-Neuve (Nationale 4) indicated high rates of individual size growth. Our results point to the importance of linear landscape structure in the invasion dynamics of *Fallopia* taxa. However, we did not test for a potential relationship between linear networks, especially roads, and habitat types. As a result, we could not determine whether habitat selection and road networks were independent. Ruderal habitats may be associated with roads more than others, supporting the increased frequency of *F. japonica* and *F. × bohemica* in this habitat type. However, we have no data to support this inference and it is therefore only speculative.

Examination of species dynamics at the landscape scale did not support two of our hypotheses. The importance of sexual reproduction in the invasion dynamics of *Fallopia* and any further advantage of *F. × bohemica* due to both vegetative and sexual reproduction was not supported. In the study landscape, the species spread dynamics was high within colonized patches while new patch colonization was low. Extension within patches was most likely due to clonality for two reasons. First data suggested all new individuals were not derived from seeds due to their increased height. Second new *F. × bohemica* did not establish in close vicinity to *F. japonica.* This would be the case if seedling emergence was the cause of spread, because all seeds generated by *F. japonica* are hybrids issued from direct crosses with *F. sachalinensis* or back cross with *F. × bohemica* (Tiébré et al. 2007b). The high potential for vegetative reproduction has long been considered responsible for the spread dynamics of *Fallopia* taxa in their introduced range (Bímová et al. 2003; Mandák et al. 2004), but this view has recently been challenged on the North American continent where hybridization is more common than on the European continent (Gammon et al. 2007; Grimsby et al. 2007). The high rate of spread was also caused by low extinction rates. Pyšek et al. (2001) demonstrated that some *Fallopia* persisted for more than a century at the same site.

Table 3 Number of individuals, population density, rate of population increase, rate of individual mortality, rate of individual emergence, mean occupied surface, total occupied surface and range of occupied surface at the upper basin of the Orneau River in Gembloux, Belgium, 2002-2003

Measurements	All *Fallopia* populations			*F. aubertii*			*F. japonica*			*F. × bohemica*			*F. sachalinensis*		
	2001	2002	2003	2001	2002	2003	2001	2002	2003	2001	2002	2003	2001	2002	2003
Number of individuals	77	129	164	3	3	3	62	107	142	11	18	18	1	1	1
Density (individuals/Km²)	6.9	11.5	14.7	0.3	0.3	0.3	5.5	9.6	12.7	1.0	1.6	1.6	0.1	0.1	0.1
Rate of emergence (%)	-	70.1	29.2	-	0.0	0.0	-	75.8	35.2	-	63.6	0.0	-	0.0	0.0
Rate of mortality (%)	-	1.3	3.1	-	0.0	0.0	-	1.6	3.7	-	0.0	0.0	-	0.0	0.0
Rate of increase (%)	-	68.1	26.7	-	0.0	0.0	-	74.1	30.9	-	63.6	0.0	-	0.0	0.0
Total surface (m²)	11538.4	13673.76	15548.6	9.0	15.0	12.2	8974.8	10679.5	12107.6	2454.6	2863.7	3305.7	100.0	115.5	123.2
Mean individual size (m²)	149.8 (147.6)	106 (169.1)	93.7 (180.3)	3.0 (1.8)	5.0 (1.5)	4.1 (2.4)	144.7 (175.6)	99.8 (165.9)	83.5 (172.1)	223.1 (175.6)	159.1 (196.8)	194.5 (235.3)	-	-	-
Range of individual size (m²)	1.0-922.8	1.0-1076.5	1.0-1386.0	1.5-5.0	3.5-6.5	1.9-6.6	1.0-922.8	1.0-1076.5	1.0-1386.0	6.0-488.8	1.0-555.0	1.3-702.0	-	-	-

Standards deviations are given in brackets

Table 4 Numbers of occupied habitat patches, extinct patches, and colonized patches for *Fallopia* species on the upper basin of the Orneau River in Gembloux, Belgium, 2001-2003

	All *Fallopia* population			*F. aubertii*			*F. japonica*			*F. × bohemica*			*F. sachalinensis*		
	2001	2002	2003	2001	2002	2003	2001	2002	2003	2001	2002	2003	2001	2002	2003
Number of occupied habitat patches	46	48	50	3	3	3	38	39	41	9	10	10	1	1	1
Number of extinct patches		1	1	0	0	0	0	1	1	0	0	0	0	0	0
Number of colonized patches		3	3	0	0	0	0	2	3	0	1	0	0	0	0

Previous studies in Belgium have demonstrated sexual reproduction in *Fallopia japon-ica,* despite its male-sterility. Clones produced numerous viable hybrid seeds originating from crosses with other parental *Fallopia* species or backcrosses with *F. × bohemica* (Tiébré et al. 2007a). High genetic variability in *F. × bohemica* suggested most adult hybrids observed in Belgium originated from sexual reproduction (Tiébré et al. 2007b). Propagule pressure at the landscape scale may be high and *F. japonica* clones produced on average 2,000 seeds/m^2 (Tiébré et al. 2007a). The surface colonized by *F. japonica* could result in seed dispersal over the landscape of approximately 14 x 10^6 seeds. Wind-dispersed seeds were found in close vicinity to the parents, but dispersal over habitat patch limits has been shown to be possible, albeit at low frequency (Tiébré et al. 2007a). High potential for hybrid seed production was reported, but led to a puzzling observation from the present study. The landscape survey did not indicate increased establishment dynamics for *F. × bohemica* plants compared to *F. japonica.* This suggested that conditions for seedling establishment might be restrictive. Nevertheless, only a small proportion of seeds are needed to develop and subsequently enhance the regeneration potential of the *Fallopia* species complex. A low proportion of seedling establishment even under substantial seed production is common in plants. Our results were incongruent with Pyšek et al. (2003) who showed increased invasive dynamics of *F. × bohemica* in the Czech Republic. Pyšek et al. (2003) argued that its higher invasive potential was due to a combination of sexual and vegetative reproduction, higher vegetative growth, and genotypic diversity of the hybrids. The differences in the two studies were likely the result of different spatial and temporal scales, and differences in methodology. The Czech study was based on herbarium specimen data and our study entailed direct field surveys. Low seedling establishment may be due to selection against unbalanced hybrids, effects of winter on seed viability, competition with native vegetation, and predation (Tiébré et al. 2007a).

CONCLUSIONS

Worldwide reduction in biodiversity warrants the rapid establishment of management priorities for invasive species control and habitat protection. In this study, we explored habitat selection and distribution dynamics of four invasive alien clonal plants in the genus *Fallopia.* Disturbed sites demonstrated enhanced recruitment, colonization and spread of *Fallopia* species. Given an assumption of habitat destruction, fragmentation, and short-term disturbance, disturbed habitats play the most important role in the distribution of alien invasive *Fallopia.* Our results point to management of disturbed habitats and ecosystems to prevent invasion by exotic alien species and the subsequent maintenance of native ecosystems. In addition, the preferential location of *Fallopia* individuals along communication networks demonstrated that efforts to control invasion may focus on priority towards a limited proportion of the landscape and should target specific actors involved in those network management.

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