Biogeographic comparisons of herbivore attack, growth and impact of Japanese knotweed between Japan and France

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Summary

1. To shed light on the process of how exotic species become invasive, it is necessary to study them both in their native and non-native ranges. Our intent was to measure differences in herbivory, plant growth and the impact on other species in *Fallopia japonica* in its native and non-native ranges.

2. We performed a cross-range full descriptive, field study in Japan (native range) and France (non-native range). We assessed DNA ploidy levels, the presence of phytophagous enemies, the amount of leaf damage, several growth parameters and the co-occurrence of *Fallopia japonica* with other plant species of herbaceous communities.

3. Invasive *Fallopia japonica* plants were all octoploid, a ploidy level we did not encounter in the native range, where plants were all tetraploid. Octoploids in France harboured far less phytophagous enemies, suffered much lower levels of herbivory, grew larger and had a much stronger impact on plant communities than tetraploid conspecifics in the native range in Japan.

4. Our data confirm that *Fallopia japonica* performs better – plant vigour and dominance in the herbaceous community – in its non-native than its native range. Because we could not find octoploids in the native range, we cannot separate the effects of differences in ploidy from other biogeographic factors. To go further, common garden experiments would now be needed to disentangle the proper role of each factor, taking into account the ploidy levels of plants in their native and non-native ranges.

5. *Synthesis.* As the process by which invasive plants successfully invade ecosystems in their non-native range is probably multifactorial in most cases, examining several components – plant growth, herbivory load, impact on recipient systems – of plant invasions through biogeographic comparisons is important. Our study contributes towards filling this gap in the research, and it is hoped that this method will spread in invasion ecology, making such an approach more common.

Key-words: competition, enemy release hypothesis, *Fallopia japonica* (Japanese knotweed), invasion ecology, plant communities, plant–herbivore interactions, polyploidy

Introduction

Much research has been done to understand invasion processes and the underlying mechanisms responsible for the success of invasive species (Richardson & Pysek 2006; Catford, Jansson & Nilsson 2009; Gurevitch *et al.* 2011).

Invasion ecology has long been investigating the biological characteristics that make species invasive out of their native range (in particular -history traits, see Thompson, Hodgson & Rich 1995; Crawley, Harvey & Purvis 1996; Rejmanek & Richardson 1996; Williamson & Fitter 1996; phenotypic plasticity, see Richards *et al.* 2006; Hulme 2008; Godoy, Valladares & Castro-Diez 2011). But the outcome of species introductions also relies on the abiotic and biotic characteristics of the novel environment: not all ecosystems are equally

invisible, and the success of one given species can vary across habitats (e.g. Barney, Di Tommaso & Weston 2005; Erfmeier & Bruelheide 2010).

One leading hypothesis for why some plants have become successful invaders is the Enemy Release Hypothesis (ERH, Keane & Crawley 2002; Colautti *et al.* 2004) which states that exotic plants are introduced in their non-native range without natural enemies, that is, herbivores (*sensu lato*) and pathogens, resulting in decreased top-down regulation and increased plant growth and/or reproduction – be it through rapid evolution (Evolution of Increased Competitive Ability hypothesis, Blossey & Nötzold 1995) or as a plastic response. Alternatively, the Biotic Resistance Hypothesis (BRH, Maron & Vilà 2001; Parker & Hay 2005) posits that exotic plants are not adapted to novel enemies encountered in the non-native range and experience strong limitation to establishment and spread. Recently, authors have distinguished between generalist and specialist enemies to refine their predictions (Joshi & Vrieling 2005; Schaffner *et al.* 2011). Even though both ERH and BRH have gained support from field and experimental assessments (Parker, Burkepile & Hay 2006), the consequences of either enemy release or biotic resistance on the distribution and abundance of plants in their non-native range are still poorly understood (but see DeWalt, Denslow & Ickes 2004 for example).

Not all exotic plants perform better in their non-native range (Thébaud & Simberloff 2001), nor do they all become more locally abundant and dominant in invaded communities (Ricciardi & Cohen 2007; Firn *et al.* 2011). Some authors have distinguished between 'weak' invaders, that is, which coexist with native species, and 'strong' invaders, that is, which become dominant in communities at the expense of native species (Ortega & Pearson 2005). Understanding plant invasions as a whole therefore requires examining novel interactions with novel neighbours (Callaway & Aschehoug 2000) and quantifying the true impact of invasive plants in communities in both their native and non-native ranges (e.g. Callaway *et al.* 2012).

To test these hypotheses, it is necessary to carry on biogeographic studies, that is, cross-range comparisons between native and invasive populations of a given species (Hierro, Maron & Callaway 2005), an approach which is becoming more common in the invasion biology literature. Nevertheless, biogeographic comparisons have long overlooked the role of polyploidy (i.e. having multiple chromosome sets) in invasion success, which has been recently proposed as an important factor (see te Beest *et al.* 2012 for an extensive review). Whatever its origin (auto- or allopolyploidization), polyploidy has important genetic, cytological, physiological, morphological and *in fine* ecological consequences (Levin 1983; Bretagnolle *et al.* 1998; Soltis & Soltis 2000; Soltis, Soltis & Tate 2004). By influencing plant fitness, it can play a major role in the outcome of plant invasions, as proved by the over-representation of polyploids amongst invasive species compared with native and non-invasive exotic species (Pandit, Pocock & Kunin 2011) and by the greater success of polyploids compared with diploids in the non-native range (Lafuma *et al.* 2003;

Schlaepfer, Edwards & Billeter 2010; Thebault *et al.* 2011). Polyploidy has to be accounted for in biogeographic studies, hence.

Biogeographic studies have investigated the role of various factors (e.g. leaf herbivory, Adams *et al.* 2009; plant-plant competition, Callaway *et al.* 2011; novel weapons, Thorpe & Callaway 2011) in plant invasion success, that certainly often results from a complex combination of these different factors – as illustrated by the significant efforts made to put different hypotheses into one single theoretical framework (Alpert 2006; Richardson & Pysek 2006; Catford, Jansson & Nilsson 2009; Gurevitch *et al.* 2011). However, such biogeographic studies have rarely addressed several components of invasion at the same time.

Here, we carried on a multifaceted study to question the role of these factors in the invasive success of the perennial geophyte *Fallopia japonica* (Houtt.) Ronse Decraene (Japanese knotweed, Polygonaceae). Native to lowlands of Japan and eastern Asia, this species has become an invasive species and a weed (sensu Richardson *et al.* 2000) in natural riparian and man-made habitats (Gerber *et al.* 2008; Aguilera *et al.* 2010; Maurel *et al.* 2010) throughout Europe and USA. Surprisingly, while the spread and impacts of *F. japonica* have been paid much attention in its non-native range, very little research has been carried out in its native range, apart from a descriptive, qualitative biogeographic comparison by Bailey (2003). *Fallopia japonica* is usually thought to perform better and to have larger impacts on plant communities in its non-native range, but to our knowledge, these assumptions have never been tested so far. Nor do we know how different herbivory load is across ranges. In addition, *F. japonica* is known to occur at different ploidy levels in both ranges (Bailey 2003). In its native range, *F. japonica* varies in ploidy, with tetraploids and octoploids collected in Japan, and hexaploids found in Korea (Kim & Park 2000). In its non-native range, only octoploids have been found in Europe, but several ploidy levels occur in the USA (Gammon *et al.* 2010). We chose to analyse these factors jointly, and we conducted a cross-range full descriptive, field study to address the following questions:

1 Could ploidy levels contribute to differences in success between native and invasive *F. japonica*?

2 Are plants less damaged by herbivores and pathogens in their non-native range or their native range?

3 Are plants more vigorous in their non-native range or their native range?

4 Does *F. japonica* outcompete other plant species in the non-native range and the native range?

Materials and methods

STUDY SPECIES

Fallopia japonica (Houtt.) (Polygonaceae) is a perennial geophyte with bamboo-like annual stems, native to Japan and eastern Asia. Several varieties of *F. japonica* are found in Japan. Among them, *F. japonica* var. *japonica* was introduced to Europe in the

mid-nineteenth century as a garden ornamental mainly (Beerling, Bailey & Conolly 1994) – later to the USA, Canada, Australia and New Zealand. The species escaped from gardens, naturalized in the wild, and after a lag phase (*c.* 40 years in Czech Republic and in UK, Pysek & Prach 1993; Pysek & Hulme 2005) expanded through the whole range, becoming widely invasive (Lowe *et al.* 2000). In both its native and non-native ranges, *F. japonica* var. *japonica* is a lowland species growing primarily on riverbanks, but also widely distributed in disturbed habitats such as wastelands or road and railway banks (Bailey 2003). For easier reading, *F. japonica* var. *japonica* will be referred to as '*F. japonica*' from hereon except where otherwise specified.

STUDY AREAS

We carried out a field study in 10 sites in Japan and eight sites in France. To limit the number of varying factors, we chose sites clumped in a region with homogenous climatic and topographic conditions within each range, and we focused on highly human-disturbed lowland areas, where *F. japonica* is common in both ranges. In the native range, we focused on the highly urbanized region of Tokyo and Kanagawa prefectures (Fig. 1) where our colleagues could select sites for us. In the non-native range, sites were located in a comparable highly urbanized area: the Greater Paris Area in France (Fig. 1). Location and geographical coordinates are summarized in Table 1.

Native range

Seven of the sites (JT1 to JT7) were located in Tokyo Prefecture (5750 inhabitants km^{-2}, Ministry of Internal Affairs and Communications, 87% urbanized areas, Bureau of Urban Development, Tokyo Metropolitan Government), mainly in the central special wards. The three others (JK8 to JK10) were located in southern Kanagawa Prefecture (3640 inhabitants km^{-2}, Ministry of Internal Affairs and Communications, 33% urbanized areas, Kanagawa Prefectural Government), about 60 km from Tokyo. The climate in the Tokyo region is humid tropical: mean annual temperature is 15.9 °C, with cool winters (10.0 °C) and hot summers (21.8 °C), annual rainfall is

1405 mm on average (means calculated over the period 1971–2000, Zaiki *et al.* 2006). The year 2008 was slightly warmer (mean annual temperature: 16.4 °C) with a wetter summer than normal (1316 mm vs. 902 mm from April to September). With the exception of JT1 (within Tokyo Metropolitan University Campus) and JK10 (in a forest roadside), all sites were abandoned urban lands, situated either on railway banks or on artificial, man-made slopes along rivers. Although we lack hard data to estimate the age of sites with accuracy, they were likely to have been stable through time in the last two decades at least.

Non-native range

The study area corresponds to the heart of the Greater Paris Area, which consists of about 70% urbanized areas (IAURIF 2003) and where human density reaches 8501 inhabitants km^{-2} vs. 112 inhabitants km^{-2} on average in France (INSEE 2006). The climate in the Paris region is temperate, oceanic with continental trends: mean annual temperature is 12.2 °C, with marked differences between summer (16.9 °C) and winter (7.5 °C), annual rainfall is 641 mm on average (means calculated over the period 1971–2010, Tank *et al.* 2002). The year 2008 was slightly warmer and dryer than normal with 12.9 °C 576 mm of rainfall. All sites (F1 to F8) consisted of abandoned urban wastelands (see Muratet *et al.* 2007 for a definition). From land-use data, we know that all wastelands were at least 25 years old, except F3 and F8, which appeared more recently (10–15 years old).

DNA PLOIDY LEVELS

Only tetraploids and octoploids have been found in Japan (Bailey 2003). However, there is no published information on the current spatial distribution of tetraploids and octoploids in Japan; therefore, we sampled Japanese populations without *a priori* knowledge of their ploidy status. By contrast, previous studies strongly suggest that only octoploids occur in Europe (Bailey 2003; Mandak *et al.* 2003); therefore, we expected sampled individuals to be all octoploids. We assessed DNA ploidy levels by flow cytometry (see Appendix S1 in
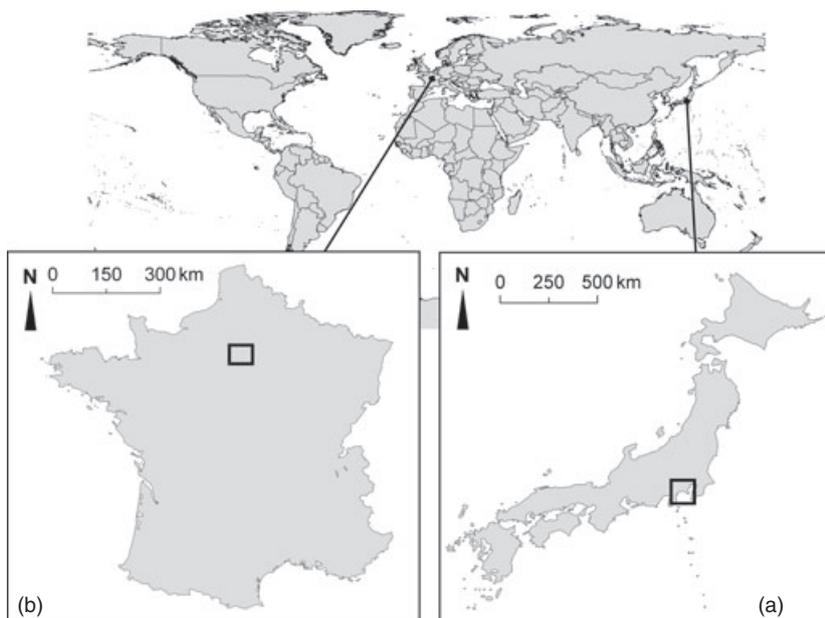

Fig. 1. Maps of the study areas. (a) Native range: Tokyo and Kanagawa prefectures, Japan; (b) Non-native range: Greater Paris Area, France.

Table 1. List of sampling sites of *Fallopia japonica* in Japan (native range) and France (non-native range) with respective geographical data

Sampling site	Location	Latitude	Longitude	Elevation (a.s.l.)
Japan				
JT1	Hachioji – Tokyo Metropolitan University campus	35°37′N	139°22′E	136 m
JT2	Tama – Tama River waterside	35°39′N	139°27′E	44 m
JT3	Tokyo, Edogawa-ku – railway slope	35°44′N	139°53′E	5 m
JT4	Ichikawa – railway slope	35°43′N	139°54′E	4 m
JT5	Tokyo, Koto-ku – railway slope	35°41′N	139°50′E	5 m
JT6	Tokyo, Katsushika-ku – Shinaka River waterside	35°44′N	139°52′E	3 m
JT7	Tokyo, Edogawa-ku – Edo River waterside	35°43′N	139°53′E	1 m
JK8	Hiratsuka – Kaname River waterside	35°21′N	139°16′E	59 m
JK9	Hiratsuka – Kaname River waterside	35°22′N	139°18′E	17 m
JK10	Hiratsuka – Hanamizu River waterside	35°19′N	139°19′E	20 m
JK11	Hadano – Kaname River waterside	35°21′N	139°14′E	64 m
JK12	Hadano – roadside on Mt. Kobo	35°22′N	139°14′E	140 m
France				
F1	Champigny-sur-Marne – roadside	48°49′N	2°31′E	74 m
F2	Châtenay-Malabry – urban wasteland	48°45′N	2°16′E	115 m
F3	Châtillon – urban bushy wasteland	48°47′N	2°16′E	134 m
F4	Colombes – urban wasteland	48°55′N	2°13′E	27 m
F5	Dugny – wasteland within urban green park	48°57′N	2°24′E	54 m
F6	Noisy-le-Grand – urban wasteland	48°50′N	2°32′E	88 m
F7	Rosny-sous-Bois – urban wasteland	48°52′N	2°30′E	112 m
F8	Rosny-sous-Bois – urban wasteland	48°52′N	2°28′E	107 m

Supporting Information for the methods) to compare cytogenetic characteristics of Japanese and French *F. japonica* patches.

DATA COLLECTION

We visited Japanese sites in late August 2008 and French sites in July and September 2008. As no significant differences were observed between the two French surveys (data not shown), all differences between French and Japanese sites were ascribed to the range and not merely to the time-lag between surveys. All the analyses presented in this study were performed using the second French data set (September).

Fallopia japonica forms patches within open vegetation formed by a continuous herbaceous cover of different heights, sometimes mixed with shrubs. When there were several patches in the same site, we chose one of them randomly to include it in our study. At each site, we placed 5 1 m² quadrats within the patch (3 in JT3, where the patch was not large enough) to collect all data mentioned hereafter.

Leaf sample

We sampled at random five leaves from each patch for flow cytometry analysis. Sampled leaves were dried and preserved in small packets in silica gel until further use.

Invertebrates

In each quadrat, we harvested invertebrates using the beating method (see Memmott *et al.* 2000 for example), that is, *F. japonica* stems were beaten over a standard-sized beating tray (110 × 80 cm). All invertebrates that fell into the cloth were collected and preserved in alcohol, with individuals from each quadrat forming a separate sample. Invertebrates were then identified and classified following their diet (Grassé 1949, 1951; Morimoto 2007; Yata 2007; Hirashima & Morimoto 2008).

Leaf damage

In each quadrat, we randomly selected three stems. On each stem, (i) we counted the leaves and estimated the percentage of damaged leaves (leaf tissue consumed by herbivores, necrosis due to attacks by fungi or pathogens) (ii) we collected and photographed the lowest leaf, an upper leaf 30 cm from the top, and a mid-height leaf. Leaf pictures were analysed with IMAGEJ software (Rasband 2003) to estimate the severity of leaf damage, as the percentage of leaf area loss (LAL, Appendix S2).

Plant growth

We assessed patch density as the number of stems in each 1 m² quadrat. We measured the length of the previously selected stems, and we counted the number of branches on the main axis. We calculated the total leaf area (TLA) based on leaf pictures described above (see 'Leaf damage' and Appendix S2 for more details).

Plant communities

Assessing the impact of invasive plant species with a synchronic approach can be problematic in the field as observed differences can be interpreted either as the invader actively changing communities/ecosystems, or merely as differences pre-existing, and controlling, the establishment of the invader. We therefore resorted to within-site comparisons with a design meant to avoid such difficulties. In each site, we assessed the co-occurrence of *F. japonica* with other species through floristic inventories conducted along four transects running from the centre of the knotweed patch towards the adjacent vegetation (Appendix S3). The more external ramets of *F. japonica* delineated the invasion front and therefore separated the invaded area ('IA', inside the patch) from the uninvaded area ('UA', outside the patch). According to the line intercept method (Canfield 1941), all vascular plant species (except *F. japonica*) that intercepted the transect line were recorded every centimetre. Transects were then split into 0.5 m sections. We calculated species richness and estimated the total cover (non-bare ground)

of the herbaceous layer, *F. japonica* excluded, in each section. See Maurel *et al.* (2010) for more details on the methods.

DATA ANALYSIS

All statistical analyses were performed using R SOFTWARE (R 2.8.0, R Development Core Team 2008). Data were transformed when required to reach normality assumption.

Leaf damage and plant growth

For each of the following variables: (i) percentage of damaged leaves, (ii) percentage of leaf area loss (LAL), (iii) stem density, (iv) stem length, (v) number of branches per stem and (vi) TLA, we tested for a range effect (non-native vs. native) using linear mixed-effect models (nlme library, Pinheiro & Bates 2000) with range as a fixed factor and site as a random factor. ANOVAS were then performed on these models.

Plant community interactions

To test whether non-invaded plant communities across ranges differed widely or were comparable, we first considered only the subset of data from uninvaded areas. We compared species richness and vegetation cover per section between Japanese sites and French sites using linear mixed-effect models with range as a fixed factor and site as a random factor.

We then considered the whole data set to assess the effect of *F. japonica* on plant communities. We analysed the variation in (i) species richness and (ii) vegetation cover calculated for each section as a function of both the range and the section location on transect (a proxy of 'invasion effect') using linear mixed-effect models, with section, range and the interaction term (informing whether an 'invasion effect' would differ between ranges or not) as fixed factors and site as a random factor. We performed an ANOVA on each model. Because patterns potentially differed across ranges, we further tested differences in species richness and vegetation cover in each range between IA and UA using Wilcoxon signed-rank tests.

Results

DNA PLOIDY LEVELS

French samples contained 9.65 ± 0.17 2 C nuclear DNA pg. In other cytological works on the invasive *Fallopia* spp., very similar values were found for European octoploid *F. japonica* plants (Suda *et al.* 2010). French samples contained twice as much nuclear DNA as Japanese samples from the study area (4.71 ± 0.04 DNA pg). Our samples were therefore interpreted as only octoploids ($8\times$, $2n = 88$) in France vs. only tetraploids ($4\times$, $2n = 44$) in Japan. No sample exhibited intermediate nuclear DNA content, which means that we correctly identified *F. japonica* and did not have hybrid *F. × bohemica* (hexaploid, $6\times$, $2n = 66$, Mandak *et al.* 2003; Suda *et al.* 2010) in our study.

INVERTEBRATE TAXA

Invertebrate taxa collected by beating *F. japonica* stems were as diverse in Japan as in France (33 vs. 27 taxa, see Table S1). On average, we observed 4.1 vs. 3.4 taxa per quadrat and 9.4 vs. 8.3 taxa per patch in Japan vs. France, respectively. Japanese and French samples differed in composition (Fig. 2). Of all taxa collected, more than two-thirds (24 taxa) were phytophagous invertebrates in Japan vs. One-third only (nine taxa) in France. Of these, 11 were identified from literature or from field observations as enemies feeding on *F. japonica* in Japan as against two taxa only (aphids and snails) in France. Among these generalists herbivores, some were frequent and sometimes locally abundant in Japanese sites, such as the scarab beetle *Anomala albopilosa albopilosa* or *Allantus luctifer* larvae. By contrast, neither phytophagous nor non-phytophagous were frequent or locally abundant in French sites.

LEAF DAMAGE

The percentage of damaged leaves in Japanese sites was about twice that observed in French sites ($91.80 \pm 1.14\%$ vs. $46.36 \pm 1.72\%$, Fig. 3a and Table 2). In Japan, this percentage frequently reached 100% (72/143 times), while this never occurred in France. Similarly, the severity of attacks by herbivores (measured through LAL) was much higher in Japanese vs. French sites ($11.37 \pm 0.81\%$ vs. $1.01 \pm 0.25\%$, Fig. 3b and Table 2).

PLANT GROWTH

Stem density did not differ significantly between the native and non-native range (27.22 ± 1.99 stems m^{-2}, Fig. 4a and Table 2). On the contrary, stems were significantly taller (266.57 ± 6.02 vs. 133.38 ± 5.41 cm, Fig. 4b and Table 2) and more ramified (8.00 ± 0.45 vs. 4.93 ± 0.36 branches per stem, Fig. 4c, and Table 2) in the non-native vs. native range. Stems barely reached 1.5 m in Japanese sites, whereas they almost systematically reached a minimum of 2.5 m in French sites. In addition, TLA tended to be higher in French vs. Japanese patches (95.56 ± 2.43 vs. 77.67 ± 2.00 cm^2, Fig. 4d and Table 2, though the relationship is only marginally significant).
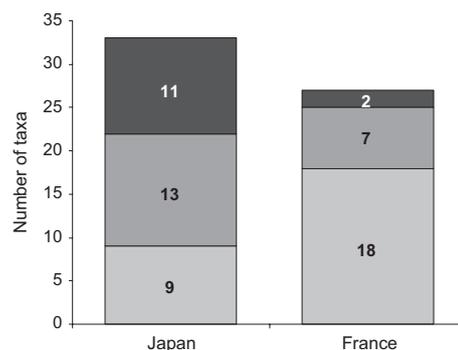

Fig. 2. Composition of invertebrate assemblages sampled on *Fallopia japonica* in Japan and France (all samples pooled). Black: number of phytophagous invertebrate taxa known to feed on *F. japonica*; dark grey: number of phytophagous invertebrate taxa not proved to feed on *F. japonica*; light grey: number of non-phytophagous invertebrate taxa. Details on invertebrate taxa are available in Table S1.
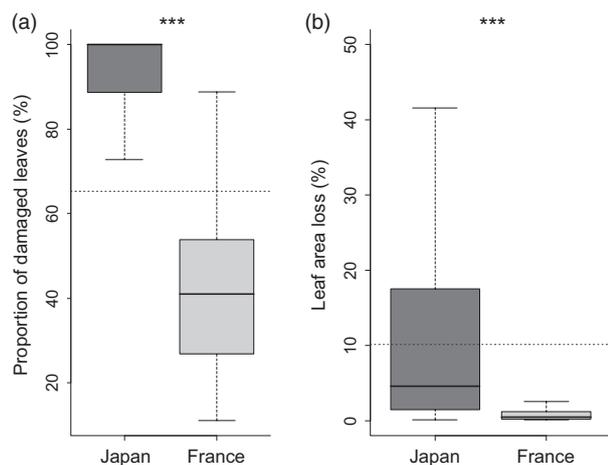
Fig. 3. Prevalence and severity of leaf damage. Proportion of damaged leaves (a) and leaf area loss (LAL, see Appendix S2) (b) expressed as percentages, in Japan and France. For each plot, the dotted line corresponds to the mean calculated on pooled data. Boxplots display the median with first and third quartiles. Statistical results are shown (***P-value < 0.001).

Table 2. Results of the anovas performed on linear mixed-effect models for all variables related to herbivory, plant growth and plant communities

Variable	Factor	d.f.	F	P
Herbivory				
Proportion of damaged leaves	Range	18	130.593	< 0.0001***
Leaf Area Loss (LAL)	Range	18	12.165	0.0033**
Plant growth				
Stem density	Range	18	0.732	0.4034 NS
Stem length	Range	18	30.209	0.0001***
No. Branches	Range	17	7.038	0.019*
Total leaf area	Range	18	5.123	0.076°
Plant communities				
Species richness	Range	18	0.949	0.344 NS
	Section	849	142.836	< 0.0001***
	Range × Section	849	93.777	< 0.0001***
Vegetation cover	Range	18	0.003	0.954 NS
	Section	849	196.625	< 0.0001***
	Range × Section	849	136.986	< 0.0001 ***

d.f., degrees of freedom; F, F-value from the ANOVA; P, P-value from the ANOVA.
Statistical results are shown as follows: NS = non-significant; °marginally significant, P-value < 0.10; *P-value < 0.05; **P-value < 0.01; and ***P-value < 0.001.

PLANT COMMUNITIES

Overall, 100 co-occurring vascular plant species were identified in Japan and 77 in France. Considering uninvaded areas only, species richness was significantly lower in Japanese vs. French sites (2.47 ± 0.08 vs. 3.38 ± 0.11 species section^{-1}, $P = 0.028$), the same trend was statistically supported for
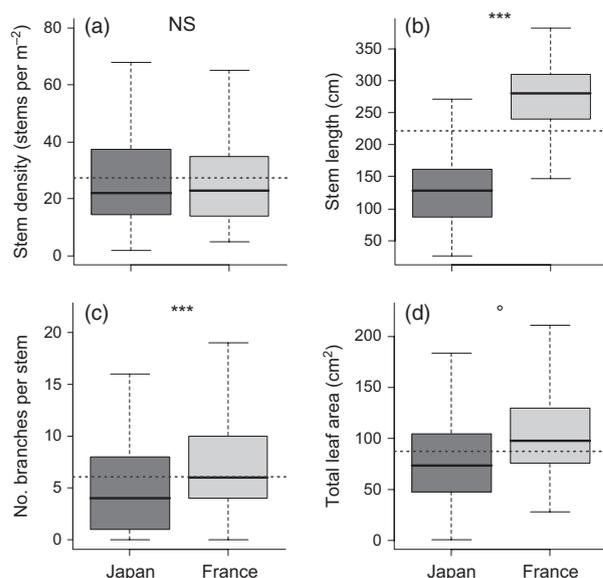

Fig. 4. Plant growth. Stem density (a), stem length (b), number of branches per stem (c) and total leaf area (d) in Japan and France. For each plot, the dotted line corresponds to the mean calculated on pooled data. Boxplots display the median with first and third quartiles. Statistical results are shown (NS = non-significant; ° = P-value < 0.1; ***P-value < 0.001).

vegetation cover (122.88 ± 4.28 vs. 186.17 ± 4.89%, $P = 0.001$). When all study sites were considered, there was no 'range' effect on species richness and vegetation cover ($P = 0.344$ and $P = 0.954$ respectively, Table 2), but the 'section' effect and the interaction term were significant in both cases ($P < 0.001$, Table 2), indicating that species richness and vegetation cover were not altered in the same way across ranges. Differences between uninvaded and invaded areas were much larger in France than in Japan: species richness and vegetation cover were reduced by 16% and 25% respectively in Japan, by 73% and 79% respectively in France (Fig. 5).

Discussion

DNA PLOIDY LEVELS

The assessment of nuclear DNA content revealed a dichotomy between tetraploid Japanese plants and octoploid French plants. The octoploidy of French plants was consistent with all previous studies carried out in Europe, where neither cytological nor genetic variation has been found among populations from various countries (Bailey 2003; Mandak *et al.* 2003, 2005). It has been inferred from this striking homogeneity that all *F. japonica* in Europe belonged to one single, highly successful, octoploid clone, issued from a plant brought back in Leiden, the Netherlands, by von Siebold in the mid-nineteenth century (Bailey & Conolly 2000).

Because by chance we did not sample octoploids in Japan, we could not assess whether they differed in performance from tetraploids in the native range, nor from octoploids of
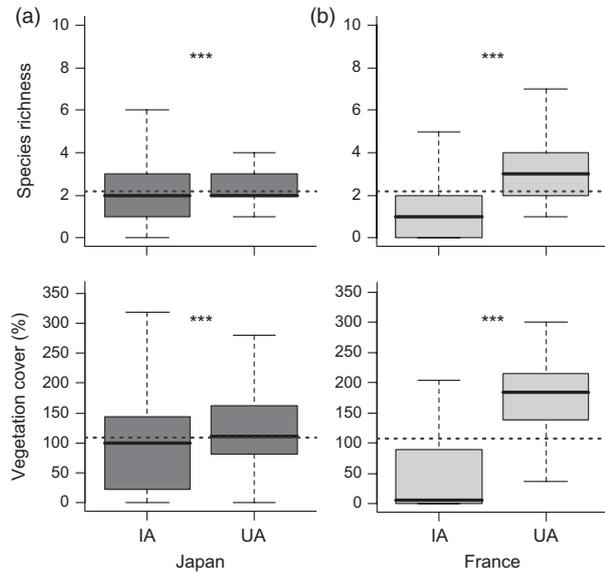
Fig. 5. Within-site differences in floristic richness and vegetation cover of plant communities (*Fallopia japonica* excluded) between invaded (IA) and uninvaded (UA) areas across ranges [Japan (a) and France (b)]. For each plot, the dotted line corresponds to the mean calculated on pooled data. Boxplots display the median with first and third quartiles. Statistical results are shown (***P-value < 0.001).

the non-native range. Strikingly, native octoploids have not supplanted native tetraploids, at least in this region. Other species demonstrate this pattern of several ploidy levels co-existing in the native, but not in the non-native range (e.g. *Senecio inaequidens*, Lafuma *et al.* 2003; *Centaurea stoebe*, Broz *et al.* 2009). This can be explained by 'pre-adaptation', that is, differences in fitness and/or competitive ability in the native range can result in the preferential success of higher vs. lower ploidy levels in the non-native range (Schlaepfer, Edwards & Billeter 2010; Thebault *et al.* 2011; te Beest *et al.* 2012). Alternatively, different cytotypes can also follow distinct evolutionary paths in the non-native range, with higher ploidy levels gaining characteristics that favour their establishment and expansion. For *F. japonica*, it is not even clear whether octoploids occur as frequently as tetraploids in Japan. It might be that octoploids are rarer than tetraploids in the native range for they produce a greater amount of defence compounds and are therefore disproportionately suppressed by specialist herbivores attracted to them. In the non-native range where no specialist enemy has co-evolved with any *F. japonica*, octoploids, unlike tetraploids, might find in high levels of defence compounds an efficient weapon against generalist herbivores.

ENEMY RELEASE AND LOWER HERBIVORY IN THE NON-NATIVE RANGE

Invertebrate abundance was far lower in French vs. Japanese patches, echoing similar observations on the effect of *F. japonica* on several taxonomic and functional groups in the below-ground and above-ground macrofauna (Bailey 2003; Gerber

et al. 2008; Topp, Kappes & Rogers 2008). Based on the identified taxa, we found that the French invertebrate communities were as diverse as the Japanese ones, but with marked differences in composition: herbivores formed an important part of the fauna sampled on Japanese plants, whereas there were almost none on French plants, either because they failed to grow on *F. japonica* (Tallamy, Ballard & D'Amico 2010) or because they avoided *F. japonica* patches because of unpalatable leaves (Krebs *et al.* 2011). Surprisingly, we sampled only generalist herbivores, even in Japan, while specialist species are usually dominant (Bernays & Graham 1988). This may be due to the fact that we sampled folivores, not internal feeders which are generally more host-specialized (Fenner & Lee 2001). Some authors estimated that it takes 100 years on average for generalists to adopt a new host (Southwood 2008). Though *F. japonica* was introduced more than 150 years ago in Europe, local phytophagous invertebrates have failed to extend their diet to this species, as reported in other cases (Siemann, Rogers & DeWalt 2006). This may be related to the absence of closely phylogenetically related species (*Fallopia* section *Reynoutria*) or of ecological counterparts (rhizomatous geophyte with large standing biomass) in the native flora of the non-native range. The quasi-absence of herbivores in the non-native range resulted in much lower leaf damage in invasive patches compared with native ones, as previously observed in natural populations for *Silene latifolia*, *Hypericum perforatum*, *Buddleja davidii* or *Acer platanoides* (Wolfe 2002; Vilà, Maron & Marco 2005; Ebeling, Hensen & Auge 2008; Adams *et al.* 2009). Therefore, our data support the ERH, not the BRH, for *F. japonica*. This escape from herbivores in the non-native range could result in higher invasiveness (Cappuccino & Carpenter 2005).

LONGER STEMS, LARGER LEAVES: INCREASED VIGOUR IN THE NON-NATIVE RANGE

Surprisingly, despite possible important differences in the genetic structure (one clone vs. genetically distinct populations), we found similar variance in all measures performed in Japanese and French *F. japonica* plants. Stem density in *F. japonica* patches varied across sites irrespective of range. More generally, the arrangement and spread of *F. japonica* patches were very comparable in Japanese and French sites, depending mainly on local environmental factors such as soil and space availability (personal observation). However, not only were stems longer, more ramified, and with more leaves in French sites, but leaves were also slightly larger than in Japanese sites. Such morphological differences resulted in a higher global photosynthetic area. One can expect major consequences from this on related physiological processes: through increased net photosynthesis, *F. japonica* could assimilate more carbon, which contributes to its overall growth rate and biomass production.

Mere differences in climatic conditions could drive such differences in growth across ranges. However, one could expect annual stem growth to be faster and larger under the warmer and wetter summer conditions of the Japanese sites, *a fortiori*

in the year 2008, which was dryer in Paris vs. wetter in Tokyo than normal. The fact that we observed the exact opposite pattern tends to rule out the hypothesis of a prominent role of climate in the very significant 'range effect'. For *Solidago gigantea*, climatic variables explained only a small proportion of the pronounced differences observed in plant size and growth between Europe and North America (Jakobs, Weber & Edwards 2004). The better performance of *F. japonica* in its non-native range can also be seen as a plastic response to a more benign biotic environment: when plants are no more top-down controlled by enemies, they can grow bigger. This might well explain the increased vigour in European *F. japonica*. Yet, as it is impossible from field data to resolve the question, reciprocal common garden experiments in different environments are required to disentangle environmental effects vs. evolutionary changes (Moloney *et al.* 2009). In addition to enemy release, polyploidy also might contribute to enhance growth potential. To clarify whether polyploidy has played a role in *F. japonica* invasion, further research is needed. In particular, our field survey should be extended to Japanese octoploids to test for performance differences between ploidy levels within the native range. Moreover, an insight into the performance of different ploidy levels from the North American part of the non-native range might nicely improve our understanding of the role of polyploidy.

CONTRASTING IMPACTS ON PLANT COMMUNITIES ACROSS RANGES

In both the native and non-native range, vegetation was significantly poorer and sparser under *F. japonica* than in the surroundings. However, this pattern was much more marked in French than in Japanese patches, indicating a much stronger impact of *F. japonica* on plant communities in the non-native than native range, consistently with previous studies in Europe (Aguilera *et al.* 2010; Maurel *et al.* 2010). The increased vigour of *F. japonica* discussed above is likely to play a critical role by giving a competitive advantage over co-occurring species in the non-native range. The effect could be all the larger as in the non-native range *F. japonica* has a propensity to sprout earlier in spring than most other species: in Great Britain shoot extension begins from early March and stems attain their maximum height mid-June (Beerling, Bailey & Conolly 1994). *F. japonica* is thus able to form rapidly dense patches, hence outshading co-occurring plants and outcompeting them for light access.

A similar impact was found on soil seed bank communities, not only by *F. japonica* but also by two other invasive plant species sharing in common large standing biomass and the formation of dense patches (Gioria & Osborne 2010). To better understand what species alter communities and ecosystems, and how much, it is not sufficient to assess impact in the non-native range, but it is crucial to compare it with impact in the native range, an aspect that is still sorely lacking in invasion ecology, including in biogeographic studies (but see Callaway *et al.* 2012). In particular, studying how invasive plants compete with co-occurring species in their native and in their non-native range could be of great help to understand the mechanisms behind impact patterns of plant invasions (see for example the experiments by Callaway *et al.* 2011; Inderjit *et al.* 2011).

Conclusion

Our field study of *F. japonica* illustrates the contribution of multifaceted biogeographic approaches to the study of invasion patterns and processes. In most cases, the success of invasive species in their non-native range is the result of a complex interplay between several of the numerous factors that have been invoked so far in the invasion literature. Focusing on one given mechanism allows going deeper into its understanding. However, to avoid missing part of the puzzle and to pave the way towards a more integrative understanding of such interplay, we highlight the relevance of biogeographic comparisons of multiple components of systems involved in invasion process.

Acknowledgements

References

Adams, J.M., Fang, W., Callaway, R.M., Cipollini, D. & Newell, E. (2009) A cross-continental test of the Enemy Release Hypothesis: leaf herbivory on *Acer platanoides* (L.) is three times lower in North America than in its native Europe. *Biological Invasions*, **11**, 1005–1016.

Aguilera, A.G., Alpert, P., Dukes, J.S. & Harrington, R. (2010) Impacts of the invasive plant *Fallopia japonica* (Houtt.) on plant communities and ecosystem processes. *Biological Invasions*, **12**, 1243–1252.

Alpert, P. (2006) The advantages and disadvantages of being introduced. *Biological Invasions*, **8**, 1523–1534.

Bailey, J. (2003) Japanese Knotweed s.l. at home and abroad. *Plant Invasions: Ecological Threats and Management Solutions* (eds L. Child, J. H. Brock, G. Brundu, K. Prach, P. Pysek, P. M. Wade & M. Williamson), pp. 183–196. Backhuys Publishers, Leiden.

Bailey, J. & Conolly, A.P. (2000) Prize-winners to pariahs – A history of Japanese Knotweed s.l (Polygonaceae) in the British Isles. *Watsonia*, **23**, 93–110.

Barney, J.N., Di Tommaso, A. & Weston, L.A. (2005) Differences in invasibility of two contrasting habitats and invasiveness of two mugwort *Artemisia vulgaris* populations. *Journal of Applied Ecology*, **42**, 567–576.

Beerling, D.J., Bailey, J.P. & Conolly, A.P. (1994) Biological flora of the British Isles Fallopia japonica (Houtt.) Ronse Decraene. *Journal of Ecology*, **82**, 959–979.

te Beest, M., Le Roux, J.J., Richardson, D.M., Brysting, A.K., Suda, J., Kubesova, M. & Pysek, P. (2012) The more the better? The role of polyploidy in facilitating plant invasions. *Annals of Botany*, **109**, 19–45.

Bernays, E. & Graham, M. (1988) On the evolution of host specificity in phytophagous arthropods. *Ecology*, **69**, 886–892.

Blossey, B. & Nötzold, R. (1995) Evolution of increased competitive ability in invasive nonindigenous plants – a hypothesis. *Journal of Ecology*, **83**, 887–889.

Bretagnolle, F., Felber, F., Calame, F.G. & Kupfer, P. (1998) Polyploidy in plants. *Botanica Helvetica*, **108**, 5–37.

Broz, A.K., Manter, D.K., Bowman, G., Muller-Scharer, H. & Vivanco, J.M. (2009) Plant origin and ploidy influence gene expression and life cycle characteristics in an invasive weed. *BMC Plant Biology*, **9**, 33.

Bureau of Urban Development, Tokyo Metropolitan Government, Available at http://www.toshiseibi.metro.tokyo.jp/. (accessed 8 September 2011)

Callaway, R.M. & Aschehoug, E.T. (2000) Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. *Science*, **290**, 521–523.

Callaway, R.M., Waller, L.P., Diaconu, A., Pal, R., Collins, A.R., Mueller-Schaerer, H. & Maron, J.L. (2011) Escape from competition: neighbors reduce *Centaurea stoebe* performance at home but not away. *Ecology*, **92**, 2208–2213.

Callaway, R.M., Schaffner, U., Thelen, G.C., Khamraev, A., Juginisov, T. & Maron, J.L. (2012) Impact of *Acroptilon repens* on co-occurring native plants is greater in the invader's non-native range. *Biological Invasions*, **14**, 1143–1155.

Canfield, R.H. (1941) Application of the line-intercept method in sampling vegetation. *Journal of Forestry*, **39**, 388–394.

Cappuccino, N. & Carpenter, D. (2005) Invasive exotic plants suffer less herbivory than non-invasive exotic plants. *Biology Letters*, **1**, 435–438.

Catford, J.A., Jansson, R. & Nilsson, C. (2009) Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Diversity and Distributions*, **15**, 22–40.

Colautti, R.I., Ricciardi, A., Grigorovich, I.A. & MacIsaac, H.J. (2004) Is invasion success explained by the enemy release hypothesis? *Ecology Letters*, **7**, 721–733.

Crawley, M.J., Harvey, P.H. & Purvis, A. (1996) Comparative ecology of the native and alien floras of the British Isles. *Philosophical Transactions of the Royal Society of London. Series B-Biological Sciences*, **351**, 1251–1259.

DeWalt, S.J., Denslow, J.S. & Ickes, K. (2004) Natural-enemy release facilitates habitat expansion of the invasive tropical shrub *Clidemia hirta*. *Ecology*, **85**, 471–483.

Ebeling, S.K., Hensen, I. & Auge, H. (2008) The invasive shrub *Buddleja davidii* performs better in its introduced range. *Diversity and Distributions*, **14**, 225–233.

Erfmeier, A. & Bruelheide, H. (2010) Invasibility or invasiveness? Effects of habitat, genotype, and their interaction on invasive Rhododendron ponticum populations. *Biological Invasions*, **12**, 657–676.

Fenner, M. & Lee, W.G. (2001) Lack of pre-dispersal seed predators in introduced Asteraceae in New Zealand. *New Zealand Journal of Ecology*, **25**, 95–99.

Firn, J., Moore, J.L., MacDougall, A.S., Borer, E.T., Seabloom, E.W., HilleRis-Lambers, J. *et al.* (2011) Abundance of introduced species at home predicts abundance away in herbaceous communities. *Ecology Letters*, **14**, 274–281.

Gammon, M.A., Baack, E., Orth, J.F. & Kesseli, R. (2010) Viability, growth, and fertility of knotweed cytotypes in North America. *Invasive Plant Science and Management*, **3**, 208–218.

Gerber, E., Krebs, C., Murrell, C., Moretti, M., Rocklin, R. & Schaffner, U. (2008) Exotic invasive knotweeds (*Fallopia* spp.) negatively affect native plant and invertebrate assemblages in European riparian habitats. *Biological Conservation*, **141**, 646–654.

Gioria, M. & Osborne, B. (2010) Similarities in the impact of three large invasive plant species on soil seed bank communities. *Biological Invasions*, **12**, 1671–1683.

Godoy, O., Valladares, F. & Castro-Diez, P. (2011) Multispecies comparison reveals that invasive and native plants differ in their traits but not in their plasticity. *Functional Ecology*, **25**, 1248–1259.

Grassé, P.P. (1949) *Traité de zoologie. Anatomie, Systématique, Biologie. Tome IX. Insectes (Paléontologie, Géonémie, Insectes inférieurs, Coléoptères)*. Masson, Paris.

Grassé, P.P. (1951) *Traité de zoologie. Anatomie, Systématique, Biologie. Tome X. Insectes (Insectes supérieurs et Hémiptéroïdes)*. Masson, Paris.

Gurevitch, J., Fox, G.A., Wardle, G.M., Inderjit & Taub, D. (2011) Emergent insights from the synthesis of conceptual frameworks for biological invasions. *Ecology Letters*, **14**, 407–418.

Hierro, J.L., Maron, J.L. & Callaway, R.M. (2005) A biogeographical approach to plant invasions: the importance of studying exotics in their introduced *and* native range. *Journal of Ecology*, **93**, 5–15.

Hirashima, Y. & Morimoto, K. (2008) *Iconographia Insectorum Japonicorum, Colore naturali edita*. **3**. Hokuryukan Co. Ltd., Tokyo.

Hulme, P.E. (2008) Phenotypic plasticity and plant invasions: is it all Jack? *Functional Ecology*, **22**, 3–7.

IAURIF (2003) *Institute for Planning and Development of the Paris Ile-de-France Region*, Available at http://www.iau-idf.fr/ (accessed 8 September 2011).

Inderjit, Evans, H., Crocoll, C., Bajpai, D., Kaur, R., Feng, Y.L., Silva, C., Carreon, J.T., Valiente-Banuet, A., Gershenzon, J. & Callaway, R.M. (2011) Volatile chemicals from leaf litter are associated with invasiveness of a Neotropical weed in Asia. *Ecology*, **92**, 316–324.

INSEE (2006) *National Institute for Statistics and Economic Studies*, Available at http://www.insee.fr/ (accessed 8 September 2011).

Jakobs, G., Weber, E. & Edwards, P.J. (2004) Introduced plants of the invasive *Solidago gigantea* (Asteraceae) are larger and grow denser than conspecifics in the native range. *Diversity and Distributions*, **10**, 11–19.

Joshi, J. & Vrieling, K. (2005) The enemy release and EICA hypothesis revisited: incorporating the fundamental difference between specialist and generalist herbivores. *Ecology Letters*, **8**, 704–714.

Kanagawa Prefectural Government, Available at http://www.pref.kanagawa.jp/ (accessed 8 September 2011).

Keane, R.M. & Crawley, M.J. (2002) Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology and Evolution*, **17**, 164–170.

Kim, J.Y. & Park, C.W. (2000) Morphological and chromosomal variation in *Fallopia* section *Reynoutria* (Polygonaceae) in Korea. *Brittonia*, **52**, 34–48.

Krebs, C., Gerber, E., Matthies, D. & Schaffner, U. (2011) Herbivore resistance of invasive *Fallopia* species and their hybrids. *Oecologia*, **167**, 1041–1052.

Lafuma, L., Balkwill, K., Imbert, E., Verlaque, R. & Maurice, S. (2003) Ploidy level and origin of the European invasive weed *Senecio inaequidens* (Asteraceae). *Plant Systematics and Evolution*, **243**, 59–72.

Levin, D.A. (1983) Polyploidy and novelty in flowering plants. *American Naturalist*, **122**, 1–25.

Lowe, S., Browne, M., Boudjelas, S. & De Poorter, M. (2000) *100 of the World's Worst Invasive Alien Species. A selection from the Global Invasive Species Database*. Published by the IUCN Invasive Species Specialist Group (ISSG). Available at http://www.issg.org/ (accessed 8 September 2011).

Mandak, B., Pysek, P., Lysak, M., Suda, J., Krahulcova, A. & Bimova, K. (2003) Variation in DNA-ploidy levels of *Reynoutria* taxa in the Czech Republic. *Annals of Botany*, **92**, 265–272.

Mandak, B., Bimova, K., Pysek, P., Stepanek, J. & Plackova, I. (2005) Isoenzyme diversity in *Reynoutria* (Polygonaceae) taxa: escape from sterility by hybridization. *Plant Systematics and Evolution*, **253**, 219–230.

Maron, J.L. & Vilà, M. (2001) When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. *Oikos*, **95**, 361–373.

Maurel, N., Salmon, S., Ponge, J.F., Machon, N., Moret, J. & Muratet, A. (2010) Does the invasive species *Reynoutria japonica* have an impact on soil and flora in urban wastelands? *Biological Invasions*, **12**, 1709–1719.

Memmott, J., Fowler, S.V., Paynter, Q., Sheppard, A.W. & Syrett, P. (2000) The invertebrate fauna on broom, *Cytisus scoparius*, in two native and two exotic habitats. *Acta Oecologica*, **21**, 213–222.

Ministry of Internal Affairs and Communication, Statistics Bureau, Available at http://www.stat.go.jp/ (accessed 8 September 2011).

Moloney, K.A., Holzapfel, C., Tielborger, K., Jeltsch, F. & Schurr, F.M. (2009) Rethinking the common garden in invasion research. *Perspectives in Plant Ecology, Evolution and Systematics*, **11**, 311–320.

Morimoto, K. (2007) *Iconographia Insectorum Japonicorum, Colore naturali edita*. **2**. Hokuryukan Co. Ltd., Tokyo.

Muratet, A., Machon, N., Jiguet, F., Moret, J. & Porcher, E. (2007) The role of urban structures in the distribution of wasteland flora in the greater Paris Area, France. *Ecosystems*, **10**, 661–671.

Ortega, Y.K. & Pearson, D.E. (2005) Weak vs. strong invaders of natural plant communities: assessing invasibility and impact. *Ecological Applications*, **15**, 651–661.

Pandit, M.K., Pocock, M.J.O. & Kunin, W.E. (2011) Ploidy influences rarity and invasiveness in plants. *Journal of Ecology*, **99**, 1108–1115.

Parker, J.D., Burkepile, D.E. & Hay, M.E. (2006) Opposing effects of native and exotic herbivores on plant invasions. *Science*, **311**, 1459–1461.

Parker, J.D. & Hay, M.E. (2005) Biotic resistance to plant invasions? Native herbivores prefer non-native plants. *Ecology Letters*, **8**, 959–967.

Pinheiro, J.C. & Bates, D.M.(2000) *Mixed-Effects Models in S and S-PLUS*. Springer, New York.

Pysek, P. & Hulme, P.E. (2005) Spatio-temporal dynamics of plant invasions: linking pattern to process. *Ecoscience*, **12**, 302–315.

Pysek, P. & Prach, K. (1993) Plant invasions and the role of riparian habitats – A comparison of 4 species alien to central Europe. *Journal of Biogeography*, **20**, 413–420.

R Development Core Team (2008) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna. Available at http://www.R-project.org/.

Rasband, W. (2003) *Image J*. National Institutes of Health, Bethesda, Maryland.

Rejmanek, M. & Richardson, D.M. (1996) What attributes make some plant species more invasive? *Ecology*, **77**, 1655–1661.

Ricciardi, A. & Cohen, J. (2007) The invasiveness of an introduced species does not predict its impact. *Biological Invasions*, **9**, 309–315.

Richards, C.L., Bossdorf, O., Muth, N.Z., Gurevitch, J. & Pigliucci, M. (2006) Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. *Ecology Letters*, **9**, 981–993.

Richardson, D.M. & Pysek, P. (2006) Plant invasions: merging the concepts of species invasiveness and community invasibility. *Progress in Physical Geography*, **30**, 409–431.

Richardson, D.M., Pysek, P., Rejmanek, M., Barbour, M.G., Panetta, F.D. & West, C.J. (2000) Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions*, **6**, 93–107.

Schaffner, U., Ridenour, W.M., Wolf, V.C., Bassett, T., Muller, C., Muller-Scharer, H., Sutherland, S., Lortie, C.J. & Callaway, R.M. (2011) Plant invasions, generalist herbivores, and novel defense weapons. *Ecology*, **92**, 829–835.

Schlaepfer, D.R., Edwards, P.J. & Billeter, R. (2010) Why only tetraploid *Solidago gigantea* (Asteraceae) became invasive: a common garden comparison of ploidy levels. *Oecologia*, **163**, 661–673.

Siemann, E., Rogers, W.E. & DeWalt, S.J. (2006) Rapid adaptation of insect herbivores to an invasive plant. *Proceedings of the Royal Society B-Biological Sciences*, **273**, 2763–2769.

Soltis, P.S. & Soltis, D.E. (2000) The role of genetic and genomic attributes in the success of polyploids. *Proceedings of the National Academy of Sciences of the United States of America*, **97**, 7051–7057.

Soltis, D.E., Soltis, P.S. & Tate, J.A. (2004) Advances in the study of polyploidy since Plant speciation. *New Phytologist*, **161**, 173–191.

Southwood, T.R.E. (2008) Insect-plant adaptations. *Ciba Foundation Symposium 102 – Origins and Development of Adaptation* (eds D. Evered & G. M. Collins), pp. 138–151. John Wiley & Sons, Ltd., Chichester.

Suda, J., Travnicek, P., Mandak, B. & Berchova-Bimova, K. (2010) Genome size as a marker for identifying the invasive alien taxa in *Fallopia* section *Reynoutria*. *Preslia*, **82**, 97–106.

Tallamy, D.W., Ballard, M. & D'Amico, V. (2010) Can alien plants support generalist insect herbivores? *Biological Invasions*, **12**, 2285–2292.

Tank, A., Wijngaard, J.B., Konnen, G.P., Bohm, R., Demaree, G., Gocheva, A. et al. (2002) Daily dataset of 20th-century surface air temperature and precipitation series for the European Climate Assessment. *International Journal of Climatology*, **22**, 1441–1453.

Thébaud, C. & Simberloff, D. (2001) Are plants really larger in their introduced ranges? *American Naturalist*, **157**, 231–236.

Thebault, A., Gillet, F., Muller-Scharer, H. & Buttler, A. (2011) Polyploidy and invasion success: trait trade-offs in native and introduced cytotypes of two Asteraceae species. *Plant Ecology*, **212**, 315–325.

Thompson, K., Hodgson, J.G. & Rich, T.C.G. (1995) Native and alien invasive plants: more of the same? *Ecography*, **18**, 390–402.

Thorpe, A.S. & Callaway, R.M. (2011) Biogeographic differences in the effects of *Centaurea stoebe* on the soil nitrogen cycle: novel weapons and soil microbes. *Biological Invasions*, **13**, 1435–1445.

Topp, W., Kappes, H. & Rogers, F. (2008) Response of ground-dwelling beetle (Coleoptera) assemblages to giant knotweed (*Reynoutria* spp.) invasion. *Biological Invasions*, **10**, 381–390.

Vilà, M., Maron, J.L. & Marco, L. (2005) Evidence for the enemy release hypothesis in *Hypericum perforatum*. *Oecologia*, **142**, 474–479.

Williamson, M.H. & Fitter, A. (1996) The characters of successful invaders. *Biological Conservation*, **78**, 163–170.

Wolfe, L.M. (2002) Why alien invaders succeed: support for the escape-from-enemy hypothesis. *American Naturalist*, **160**, 705–711.

Yata, O.(2007) *Iconographia Insectorum Japonicorum, Colore naturali edita*. **1**. Hokuryukan Co. Ltd., Tokyo.

Zaiki, M., Konnen, G.P., Tsukahara, T., Jones, P.D., Mikami, T. & Matsumoto, K. (2006) Recovery of nineteenth-century Tokyo/Osaka meteorological data in Japan. *International Journal of Climatology*, **26**, 399–423.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Nuclear DNA ploidy content assessment by flow cytometry.

Appendix S2. Assessment of Leaf Area Loss (LAL) and Total Leaf Area (TLA) by analysing leaf pictures with ImageJ software.

Appendix S3. Schematic representation of the sampling design used for floristic inventories.

Table S1. List of all invertebrates harvested on *Fallopia japonica* in Japanese and French sites, with the damage they may cause to *F. japonica* according to literature data and to expert knowledge.