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► **To cite this version:**

Noëlie Maurel, Maasaki Fujiyoshi, Audrey Muratet, Emmanuelle Porcher, Eric Motard, et al.. Biogeographic comparisons of herbivore attack, growth and impact of Japanese knotweed between Japan and France. *Journal of Ecology*, 2013, 101 (1), pp.118-127. 10.1111/1365-2745.12026 . mnhn-02265411

**HAL Id: mnhn-02265411**

**<https://mnhn.hal.science/mnhn-02265411v1>**

Submitted on 9 Aug 2019

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

3

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16

17 ***Running headline: Japanese knotweed in its native and non-native range***

18

19

20

## 21 **Summary**

- 22 1. In order to shed light on the process of how exotic species become invasive, it is necessary to study them  
23 both in their native and non-native ranges. Our purpose was to measure differences in herbivory, plant  
24 growth, and the impact on other species in *Fallopia japonica* in its native and non-native ranges.
- 25 2. We performed a cross-range full descriptive, field study in Japan (native range) and France (non-native  
26 range). We assessed DNA ploidy levels, the presence of phytophagous enemies, the amount of leaf damage,  
27 several growth parameters, and the co-occurrence of *Fallopia japonica* with other plant species of  
28 herbaceous communities.
- 29 3. Invasive *Fallopia japonica* plants were all octoploid, a ploidy level we did not encounter in the native range,  
30 where plants were all tetraploid. Octoploids in France harboured far less phytophagous enemies, suffered  
31 much lower levels of herbivory, grew larger and had a much stronger impact on plant communities than  
32 tetraploid conspecifics in the native range in Japan.
- 33 4. Our data confirm that *Fallopia japonica* performs better – plant vigour and dominance in the herbaceous  
34 community – in its non-native than its native range. Because we could not find octoploids in the native  
35 range, we cannot separate the effects of differences in ploidy from other biogeographic factors. To go  
36 further, common garden experiments would now be needed to disentangle the proper role of each factor,  
37 taking into account the ploidy levels of plants in their native and non-native ranges.
- 38 5. *Synthesis*. As the process by which invasive plants successfully invade ecosystems in their non-native range  
39 is probably multifactorial in most cases, examining several components – plant growth, herbivory load,  
40 impact on recipient systems – of plant invasions through biogeographic comparisons is important. Our study  
41 contributes towards filling this gap in the research and it is hoped that this method will spread in invasion  
42 ecology, making such an approach more common.

43

### 44 **Key-words**

45 competition, Enemy Release Hypothesis (ERH), *Fallopia japonica* (Japanese knotweed), invasion ecology,  
46 plant communities, plant-herbivore interactions, polyploidy

47

## 48 **Introduction**

49

50        Much research has been done to understand invasion processes and the underlying mechanisms  
51 responsible for the success of invasive species (Richardson and Pysek 2006; Catford *et al.* 2009; Gurevitch *et al.*  
52 2011). Invasion ecology has long been investigating the biological characteristics that make species invasive out  
53 of their native range (in particular life-history traits, see Thompson *et al.* 1995; Crawley *et al.* 1996; Rejmanek  
54 and Richardson 1996; Williamson and Fitter 1996; phenotypic plasticity, see Richards *et al.* 2006; Hulme 2008;  
55 Godoy *et al.* 2011). But the outcome of species introductions also relies on the abiotic and biotic characteristics  
56 of the novel environment: not all ecosystems are equally invasible, and the success of one given species can vary  
57 across habitats (e.g. Barney *et al.* 2005; Erfmeier and Bruehlheide 2010).

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

70        Not all exotic plants perform better in their non-native range (Thébaud and Simberloff 2001), nor do they  
71 all become more locally abundant and dominant in invaded communities (Ricciardi and Cohen 2007; Firn *et al.*  
72 2011). Some authors have distinguished between “weak” invaders, i.e. which coexist with native species, and  
73 “strong” invaders, i.e. which become dominant in communities at the expense of native species (Ortega and  
74 Pearson 2005). Understanding plant invasions as a whole therefore requires examining novel interactions with  
75 novel neighbours (Callaway and Aschehoug 2000) and quantifying the true impact of invasive plants in  
76 communities in both their native and non-native ranges (e.g. Callaway *et al.* 2012).

77 To test these hypotheses, it is necessary to carry on biogeographic studies, i.e. cross-range comparisons  
78 between native and invasive populations of a given species (Hierro *et al.* 2005), an approach which is becoming  
79 more common in the invasion biology literature. Nevertheless, biogeographic comparisons have long overlooked  
80 the role of polyploidy (i.e. having multiple chromosome sets) in invasion success, which has been recently  
81 proposed as an important factor (see te Beest *et al.* 2012 for an extensive review). Whatever its origin (auto- or  
82 allopolyploidization), polyploidy has important genetic, cytological, physiological, morphological and *in fine*  
83 ecological consequences (Levin 1983; Bretagnolle *et al.* 1998; Soltis and Soltis 2000; Soltis *et al.* 2004). By  
84 influencing plant fitness, it can play a major role in the outcome of plant invasions, as proved by the over-  
85 representation of polyploids amongst invasive species compared to native and non-invasive exotic species  
86 (Pandit *et al.* 2011) and by the greater success of polyploids compared to diploids in the non-native range  
87 (Lafuma *et al.* 2003; Schlaepfer *et al.* 2010; Thebault *et al.* 2011). Polyploidy has to be accounted for in  
88 biogeographic studies, hence.

89 Biogeographic studies have investigated the role of various factors (e.g. leaf herbivory, Adams *et al.*  
90 2009; plant-plant competition, Callaway *et al.* 2011; novel weapons, Thorpe and Callaway 2011) in plant  
91 invasion success, that certainly often result from a complex combination of these different factors – as illustrated  
92 by the significant efforts made to put different hypotheses into one single theoretical framework (Alpert 2006;  
93 Richardson and Pysek 2006; Catford *et al.* 2009; Gurevitch *et al.* 2011). However, such biogeographic studies  
94 have rarely addressed several components of invasion at the same time.

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

107 ploidy levels occur in the USA (Gammon *et al.* 2010). We chose to analyse these factors jointly and we  
108 conducted a cross-range full descriptive, field study to address the following questions:

109

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

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

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

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

114

## 115 **Materials and Methods**

116

### 117 *Study species*

118 *Fallopia japonica* (Houtt.) (Polygonaceae) is a perennial geophyte with bamboo-like annual stems, native  
119 to Japan and eastern Asia. Several varieties of *F. japonica* are found in Japan. Among them, *F. japonica* var.  
120 *japonica* was introduced to Europe in the mid-nineteenth century as a garden ornamental mainly (Beerling *et al.*  
121 1994) – later to the USA, Canada, Australia and New Zealand. The species escaped from gardens, naturalised in  
122 the wild, and after a lag phase (~40 years in Czech Republic and in UK, Pysek and Prach 1993; Pysek and  
123 Hulme 2005) expanded through the whole range, becoming widely invasive (Lowe *et al.* 2000). In both its native  
124 and non-native ranges, *F. japonica* var. *japonica* is a lowland species growing primarily on riverbanks, but also  
125 widely distributed in disturbed habitats such as wastelands or road and railway banks (Bailey 2003). For easier  
126 reading, *F. japonica* var. *japonica* will be referred to as “*F. japonica*” from hereon except where otherwise  
127 specified.

128

### 129 *Study areas*

130 We carried out a field study in 10 sites in Japan and 8 sites in France. In order to limit the number of  
131 varying factors, we chose sites clumped in a region with homogenous climatic and topographic conditions within  
132 each range and we focused on highly human-disturbed lowland areas, where *F. japonica* is common in both  
133 ranges. In the native range, we focused on the highly urbanised region of Tokyo and Kanagawa prefectures (Fig.  
134 1) where our colleagues could select sites for us. In the non-native range, sites were located in a comparable  
135 highly urbanised area: the Greater Paris Area in France (Fig. 1). Location and geographic coordinates are  
136 summarized in Table 1.

### 137 *Native range*

138 Seven of the sites (JT1 to JT7) were located in Tokyo Prefecture (5,750 inhabitants.km<sup>2</sup>, Ministry of  
139 Internal Affairs and Communications, 87% urbanised areas, Bureau of Urban Development, Tokyo Metropolitan  
140 Government), mainly in the central special wards. The 3 others (JK8 to JK10) were located in southern  
141 Kanagawa Prefecture (3,640 inhabitants.km<sup>2</sup>, Ministry of Internal Affairs and Communications, 33% urbanised  
142 areas, Kanagawa Prefectural Government), about 60 km from Tokyo. The climate in the Tokyo region is humid  
143 tropical: mean annual temperature is 15.9°C, with cool winters (10.0°C) and hot summers (21.8°C), annual  
144 rainfall is 1405 mm on average (means calculated over the period 1971–2000, Zaiki *et al.* 2006). The year 2008

145 was slightly warmer (mean annual temperature: 16.4°C) with a wetter summer than normal (1316 mm vs. 902  
146 mm from April to September). With the exception of JT1 (within Tokyo Metropolitan University Campus) and  
147 JK10 (in a forest roadside), all sites were abandoned urban lands, situated either on railway banks or on artificial,  
148 man-made slopes along rivers. Although we lack hard data to estimate the age of sites with accuracy, they were  
149 likely to have been stable through time in the last two decades at least.

#### 150 *Non-native range*

151 The study area corresponds to the heart of the Greater Paris Area, which consists of about 70% urbanised  
152 areas (IAURIF 2003) and where human density reaches 8,501 inhabitants. km<sup>-2</sup> vs. 112 inhabitants km<sup>-2</sup> on  
153 average in France (INSEE 2006). The climate in the Paris region is temperate, oceanic with continental trends:  
154 mean annual temperature is 12.2 °C, with marked differences between summer (16.9°C) and winter (7.5°C),  
155 annual rainfall is 641mm on average (means calculated over the period 1971–2010, Tank *et al.* 2002). The year  
156 2008 was slightly warmer and dryer than normal with 12.9°C 576 mm of rainfall. All sites (F1 to F8) consisted  
157 of abandoned urban wastelands (see Muratet *et al.* 2007 for a definition). From land use data, we know that all  
158 wastelands were at least 25 years old, except F3 and F8, which appeared more recently (10 to 15 years old).

159

#### 160 *DNA ploidy levels*

161 Only tetraploids and octoploids have been found in Japan (Bailey 2003). However, there is no published  
162 information on the current spatial distribution of tetraploids and octoploids in Japan, therefore we sampled  
163 Japanese populations without *a priori* knowledge of their ploidy status. By contrast, previous studies strongly  
164 suggest that only octoploids occur in Europe (Bailey 2003; Mandak *et al.* 2003), therefore we expected sampled  
165 individuals to be all octoploids. We assessed DNA ploidy levels by flow cytometry (see Appendix S1 in  
166 Supporting Information for the methods) to compare cytogenetic characteristics of Japanese and French *F.*  
167 *japonica* patches.

168

#### 169 *Data collection*

170 We visited Japanese sites in late August 2008 and French sites in July and September 2008. Since no  
171 significant differences were observed between the two French surveys (data not shown), all differences between  
172 French and Japanese sites were ascribed to the range and not merely to the time lag between surveys. All the  
173 analyses presented in this paper were performed using the second French dataset (September).



174 *F. japonica* forms patches within open vegetation formed by a continuous herbaceous cover of different  
175 heights, sometimes mixed with shrubs. When there were several patches in the same site, we chose one of them  
176 randomly to include it in our study. At each site, we placed 5 1 m<sup>2</sup> quadrats within the patch (3 in JT3, where the  
177 patch was not large enough) to collect all data mentioned hereafter.

#### 178 *Leaf sample*

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

#### 181 *Invertebrates*

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

#### 187 *Leaf damage*

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

#### 193 *Plant growth*

194 We assessed patch density as the number of stems in each 1 m<sup>2</sup> quadrat. We measured the length of the  
195 previously-selected stems and we counted the number of branches on the main axis. We calculated the total leaf  
196 area (TLA) based on leaf pictures described above (see 'Leaf damage' and Appendix S2 for more details).

#### 197 *Plant communities*

198 Assessing the impact of invasive plant species with a synchronic approach can be problematic in the field  
199 since observed differences can be interpreted either as the invader actively changing communities/ecosystems, or  
200 merely as differences pre-existing, and controlling, the establishment of the invader. We therefore resorted to  
201 within-site comparisons with a design meant to avoid such difficulties. In each site, we assessed the co-  
202 occurrence of *F. japonica* with other species through floristic inventories conducted along four transects running  
203 from the centre of the knotweed patch towards the adjacent vegetation (Appendix S3). The more external ramets

204 of *F. japonica* delineated the invasion front and therefore separated the invaded area ('IA', inside the patch) from  
205 the uninvaded area ('UA', outside the patch). According to the line intercept method (Canfield 1941), all  
206 vascular plant species (except *F. japonica*) that intercepted the transect line were recorded every centimetre.  
207 Transects were then split into 0.5 m sections. We calculated species richness and estimated the total cover (non-  
208 bare ground) of the herbaceous layer, *F. japonica* excluded, in each section. See Maurel *et al.* (2010) for more  
209 details on the methods.

210

### 211 *Data analysis*

212 All statistical analyses were performed using R software (R 2.8.0, R Development Core Team 2008).

213 Data were transformed when required to reach normality assumption.

### 214 *Leaf damage and plant growth*

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

### 220 *Plant community interactions*

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

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

232

233

## 234 **Results**

### 235 *DNA ploidy levels*

236 French samples contained  $9.65 \pm 0.17$  2C nuclear DNA pg. In other cytological works on the invasive  
237 *Fallopia* spp., very similar values were found for European octoploid *F. japonica* plants (Suda *et al.* 2010).  
238 French samples contained twice as much nuclear DNA as Japanese samples from the study area ( $4.71 \pm 0.04$   
239 DNA pg). Our samples were therefore interpreted as only octoploids (8X,  $2n = 88$ ) in France vs. only tetraploids  
240 (4X,  $2n = 44$ ) in Japan. No sample exhibited intermediate nuclear DNA content, which means that we correctly  
241 identified *F. japonica* and did not have hybrid *F. x bohemica* (hexaploid, 6X,  $2n = 66$ , Mandak *et al.* 2003; Suda  
242 *et al.* 2010) in our study.

243

### 244 *Invertebrate taxa*

245 Invertebrate taxa collected by beating *F. japonica* stems were as diverse in Japan as in France (thirty-  
246 three vs. twenty-seven taxa, see Table S1). On average, we observed 4.1 vs. 3.4 taxa per quadrat and 9.4 vs. 8.3  
247 taxa per patch in Japan vs. France, respectively. Japanese and French samples differed in composition (Fig. 5).  
248 Of all taxa collected, more than two-thirds (24 taxa) were phytophagous invertebrates in Japan vs. one third only  
249 (nine taxa) in France. Of these, 11 were identified from literature or from field observations as enemies feeding  
250 on *F. japonica* in Japan as against two taxa only (aphids and snails) in France. Among these generalists  
251 herbivores, some were frequent and sometimes locally abundant in Japanese sites, such as the scarab beetle  
252 *Anomala albopilosa albopilosa* or *Allantus luctifer* larvae. By contrast, neither phytophagous nor non-  
253 phytophagous were frequent or locally abundant in French sites.

254

### 255 *Leaf damage*

256 The percentage of damaged leaves in Japanese sites was about twice that observed in French sites  
257 ( $91.80 \pm 1.14\%$  vs.  $46.36 \pm 1.72\%$ , Fig. 2a and Table 2). In Japan, this percentage frequently reached 100%  
258 (72 / 143 times), while this never occurred in France. Similarly, the severity of attacks by herbivores (measured  
259 through LAL) was much higher in Japanese vs. French sites ( $11.37 \pm 0.81\%$  vs.  $1.01 \pm 0.25\%$ , Fig. 2b and Table  
260 2).

261

### 262 *Plant growth*

263 Stem density did not differ significantly between the native and non-native range ( $27.22 \pm 1.99$  stems  $m^{-2}$ ,  
264 Fig. 3a and Table 2). On the contrary, stems were significantly taller ( $266.57 \pm 6.02$  vs.  $133.38 \pm 5.41$  cm, Fig. 3b  
265 and Table 2) and more ramified ( $8.00 \pm 0.45$  vs.  $4.93 \pm 0.36$  branches per stem, Fig. 3c, and Table 2) in the non-  
266 native vs. native range. Stems barely reached 1.5m in Japanese sites, whereas they almost systematically reached  
267 a minimum of 2.5m in French sites. In addition, TLA tended to be higher in French vs. Japanese patches  
268 ( $95.56 \pm 2.43$  vs.  $77.67 \pm 2.00$   $cm^2$ , Fig. 3d and Table 2, though the relationship is only marginally significant).

269

### 270 *Plant communities*

271 Over all, 100 co-occurring vascular plant species were identified in Japan, and 77 in France. Considering  
272 uninvaded areas only, species richness was significantly lower in Japanese vs. French sites ( $2.47 \pm 0.08$  vs.  
273  $3.38 \pm 0.11$  species section $^{-1}$ ,  $P = 0.028$ ), the same trend was statistically supported for vegetation cover  
274 ( $122.88 \pm 4.28$  vs.  $186.17 \pm 4.89\%$ ,  $P = 0.001$ ). When all study sites were considered, there was no 'range' effect  
275 on species richness and vegetation cover ( $p = 0.344$  and  $p = 0.954$  respectively, Table 2), but the 'section' effect  
276 and the interaction term were significant in both cases ( $p < 0.001$ , Table 2), indicating that species richness and  
277 vegetation cover were not altered in the same way across ranges. Differences between uninvaded and invaded  
278 areas were much larger in France than in Japan: species richness and vegetation cover were reduced by 16% and  
279 25% respectively in Japan, by 73% and 79% respectively in France (Fig. 4).

280

## 281 **Discussion**

282

### 283 *DNA-ploidy levels*

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

291         Because by chance we did not sample octoploids in Japan, we could not assess whether they differed in  
292 performance from tetraploids in the native range, nor from octoploids of the non-native range. Strikingly, native  
293 octoploids have not supplanted native tetraploids, at least in this region. Other species demonstrate this pattern of  
294 several ploidy levels co-existing in the native, but not in the non-native range (e.g. *Senecio inaequidens*, Lafuma  
295 *et al.* 2003; *Centaurea stoebe*, Broz *et al.* 2009). This can be explained by ‘pre-adaptation’, i.e. differences in  
296 fitness and/or competitive ability in the native range can result in the preferential success of higher vs. lower  
297 ploidy levels in the non-native range (Schlaepfer *et al.* 2010; Thebault *et al.* 2011; te Beest *et al.* 2012).  
298 Alternatively, different cytotypes can also follow distinct evolutionary paths in the non-native range, with higher  
299 ploidy levels gaining characteristics that favour their establishment and expansion. For *F. japonica*, it is not even  
300 clear whether octoploids occur as frequently as tetraploids in Japan. It might be that octoploids are rarer than  
301 tetraploids in the native range for they produce a greater amount of defense compounds and are therefore  
302 disproportionately suppressed by specialist herbivores attracted to them. In the non-native range where no  
303 specialist enemy has co-evolved with any *F. japonica*, octoploids, unlike tetraploids, might find in high levels of  
304 defense compounds an efficient weapon against generalist herbivores.

305

### 306 *Enemy release and lower herbivory in the non-native range*

307         Invertebrate abundance was far lower in French vs. Japanese patches, echoing similar observations on the  
308 effect of *F. japonica* on several taxonomic and functional groups in the belowground and aboveground  
309 macrofauna (Bailey 2003; Gerber *et al.* 2008; Topp *et al.* 2008). Based on the identified taxa, we found that the  
310 French invertebrate communities were as diverse as the Japanese ones, but with marked differences in

311 composition: herbivores formed an important part of the fauna sampled on Japanese plants whereas there were  
312 almost none on French plants, either because they failed to grow on *F. japonica* (Tallamy *et al.* 2010) or because  
313 they avoided *F. japonica* patches because of unpalatable leaves (Krebs *et al.* 2011). Surprisingly, we sampled  
314 only generalist herbivores, even in Japan, while specialist species are usually dominant (Bernays and Graham  
315 1988). This may be due to the fact that we sampled folivores, not internal feeders which are generally more host-  
316 specialised (Fenner and Lee 2001). Some authors estimated that it takes 100 years on average for generalists to  
317 adopt a new host (Southwood 2008). Though *F. japonica* was introduced more than 150 years ago in Europe,  
318 local phytophagous invertebrates have failed to extend their diet to this species, as reported in other cases  
319 (Siemann *et al.* 2006). This may be related to the absence of closely phylogenetically related species (*Fallopia*  
320 section *Reynoutria*) or of ecological counterparts (rhizomatous geophyte with large standing biomass) in the  
321 native flora of the non-native range. The quasi-absence of herbivores in the non-native range resulted in much  
322 lower leaf damage in invasive patches compared to native ones, as previously observed in natural populations for  
323 *Silene latifolia*, *Hypericum perforatum*, *Buddleja davidii* or *Acer platanoides* (Wolfe 2002; Vilà *et al.* 2005;  
324 Ebeling *et al.* 2008; Adams *et al.* 2009). Therefore, our data support the ERH, not the BRH, for *F. japonica*. This  
325 escape from herbivores in the non-native range could result in higher invasiveness (Cappuccino and Carpenter  
326 2005).

327

### 328 *Longer stems, larger leaves: increased vigour in the non-native range*

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

338 Mere differences in climatic conditions could drive such differences in growth across ranges. However,  
339 one could expect annual stem growth to be faster and larger under the warmer and wetter summer conditions of  
340 the Japanese sites, *a fortiori* in the year 2008 which was dryer in Paris vs. wetter in Tokyo than normal. The fact

341 that we observed the exact opposite pattern tends to rule out the hypothesis of a prominent role of climate in the  
342 very significant ‘range effect’. For *Solidago gigantea*, climatic variables explained only a small proportion of the  
343 pronounced differences observed in plant size and growth between Europe and North America (Jakobs *et al.*  
344 2004). The better performance of *F. japonica* in its non-native range can also be seen as a plastic response to a  
345 more benign biotic environment: when plants are no more top down controlled by enemies, they can grow  
346 bigger. This might well explain the increased vigour in European *F. japonica*. Yet, as it is impossible from field  
347 data to resolve the question, reciprocal common garden experiments in different environments are required to  
348 disentangle environmental effects vs. evolutionary changes (Moloney *et al.* 2009). In addition to enemy release,  
349 polyploidy also might contribute to enhance growth potential. To clarify whether polyploidy has played a role in  
350 *F. japonica* invasion, further research is needed. In particular, our field survey should be extended to Japanese  
351 octoploids to test for performance differences between ploidy levels within the native range. Moreover, an  
352 insight into the performance of different ploidy levels from the North American part of the non-native range  
353 might nicely improve our understanding of the role of polyploidy.

354

### 355 *Contrasting impacts on plant communities across ranges*

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

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

371 their non-native range could be of great help to understand the mechanisms behind impact patterns of plant  
372 invasions (see for example the experiments by Callaway *et al.* 2011; Inderjit *et al.* 2011).

373

#### 374 *Conclusion*

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

382



383 **Acknowledgements**

384 We are grateful to Pr. Jun-Ichirou Suzuki for kind, helpful recommendations in finding Tokyo study sites and to  
385 his students for their help with botanical identification. We address special thanks to Lia and Takao Sato, whose  
386 help was precious in Tokyo. We thank anonymous reviewers for their useful comments, and Ragan Callaway for  
387 his invaluable help to improve this paper. The English was edited by Stephen Gough. This project was funded by  
388 the National Museum of Natural History of Paris (PPF “Etat et structure phylogénétique de la biodiversité  
389 actuelle et fossile” 2008) and by the Région Île-de-France (R2DS 2007-12).

390

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581 **Supporting Information**

582

583 Additional supporting information may be found in the online version of this article:

584

585 **Appendix S1.** Nuclear DNA-ploidy content assessment by flow cytometry.

586

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

589

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

591

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

594

595 **Table 1**

596

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

599

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

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602 **Table 2**

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604 Results of the ANOVAs performed on linear mixed-effect models for all variables related to herbivory, plant  
 605 growth and plant communities. D.f. = degrees of freedom; F = F-value from the ANOVA; *P* = *P*-value from the  
 606 ANOVA. Statistical results are shown as follows: NS = non significant; ° = marginally significant, *P*-  
 607 value < 0.10; \* = *P*-value < 0.05; \*\* = *P*-value < 0.01; \*\*\* = *P*-value < 0.001

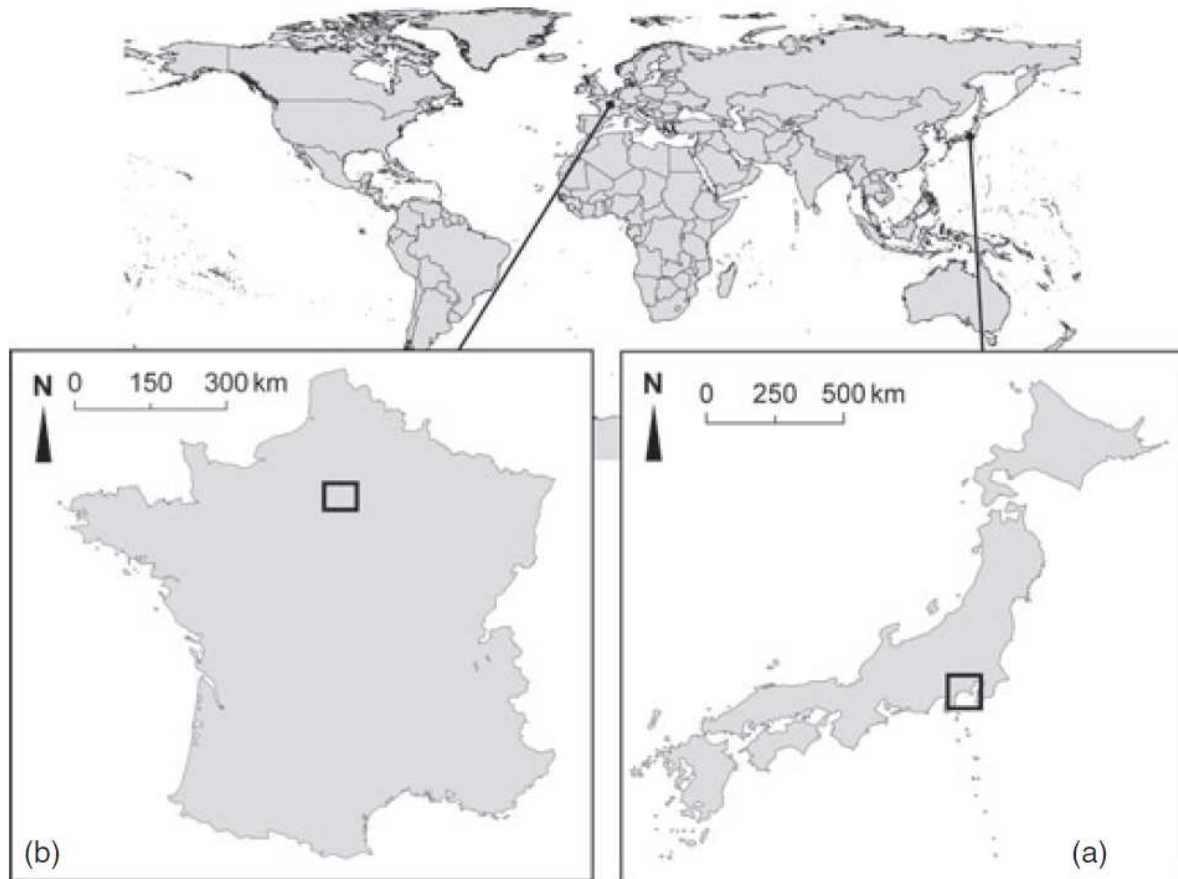
608

<b>Variable</b>	<b>Factor</b>	<b>d.f.</b>	<b>F</b>	<b><i>P</i></b>
<b><i>Herbivory</i></b>				
Proportion of damaged leaves	Range	18	130.593	<0.0001 ***
Leaf Area Loss (LAL)	Range	18	12.165	0.0033 **
<b><i>Plant growth</i></b>				
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 (TLA)	Range	18	5.123	0.076 °
<b><i>Plant communities</i></b>				
Species richness	Range	18	0.949	0.344 NS
	Section	849	142.836	<0.0001 ***
	Range x Section	849	93.777	<0.0001 ***
Vegetation cover	Range	18	0.003	0.954 NS
	Section	849	196.625	<0.0001 ***
	Range x Section	849	136.986	<0.0001 ***

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611 **Figure legends**

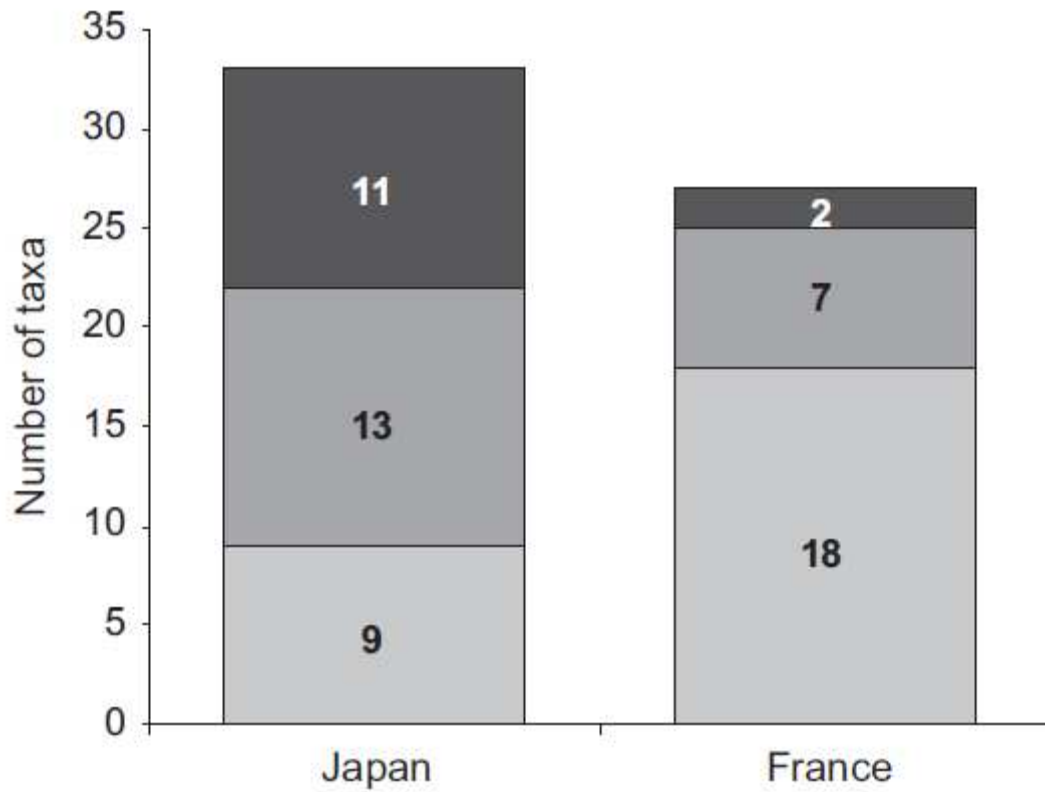


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613 **Fig 1.** Maps of the study areas. (A) Native range: Tokyo and Kanagawa prefectures, Japan; (B) Non-native  
614 range: Greater Paris Area, France.

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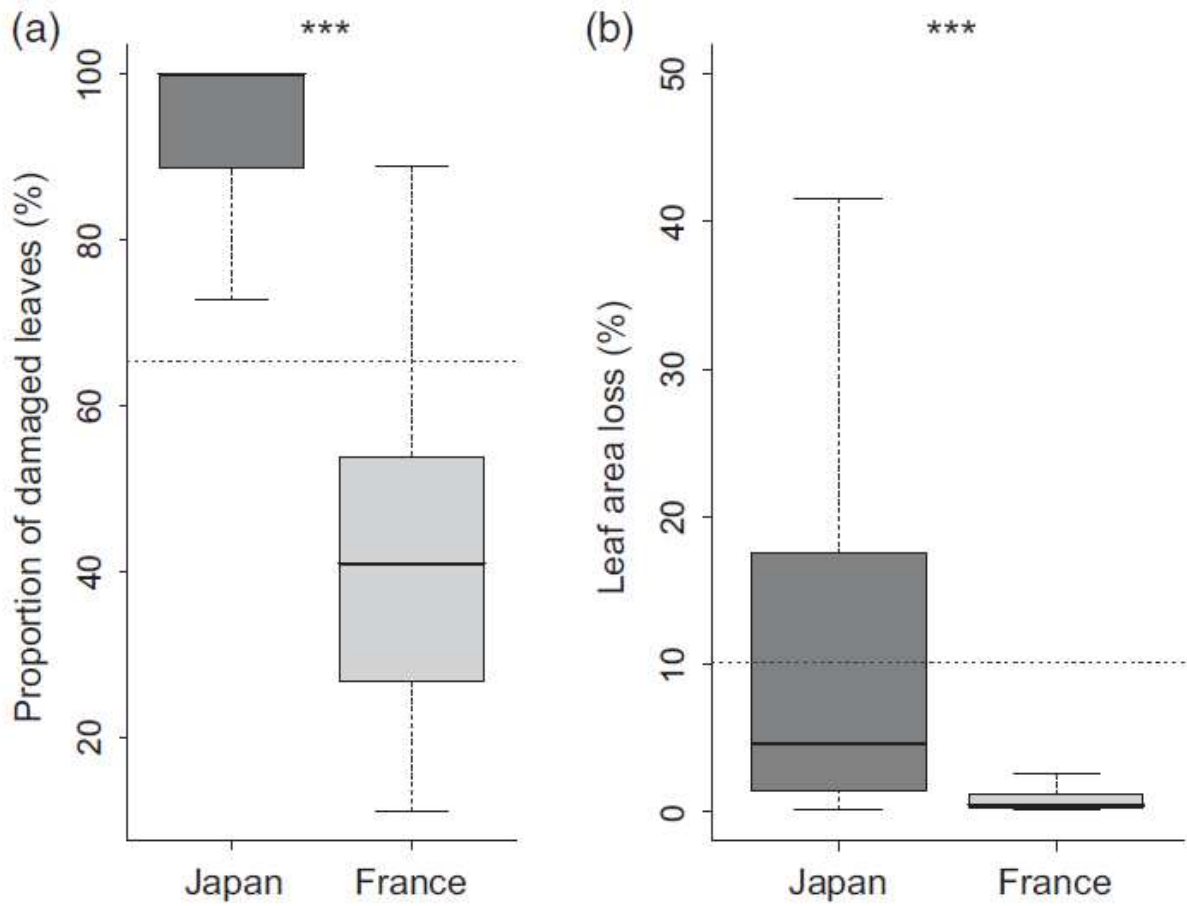
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618 **Fig 2.** Prevalence and severity of leaf damage. Proportion of damaged leaves (a) and leaf area loss (LAL, see  
 619 Appendix S2) (b) expressed as percentages, in Japan and France. For each plot, the dotted line corresponds to the  
 620 mean calculated on pooled data. Boxplots display the median with first and third quartiles. Statistical results are  
 621 shown (\*\*\*) = p-value < 0.001).

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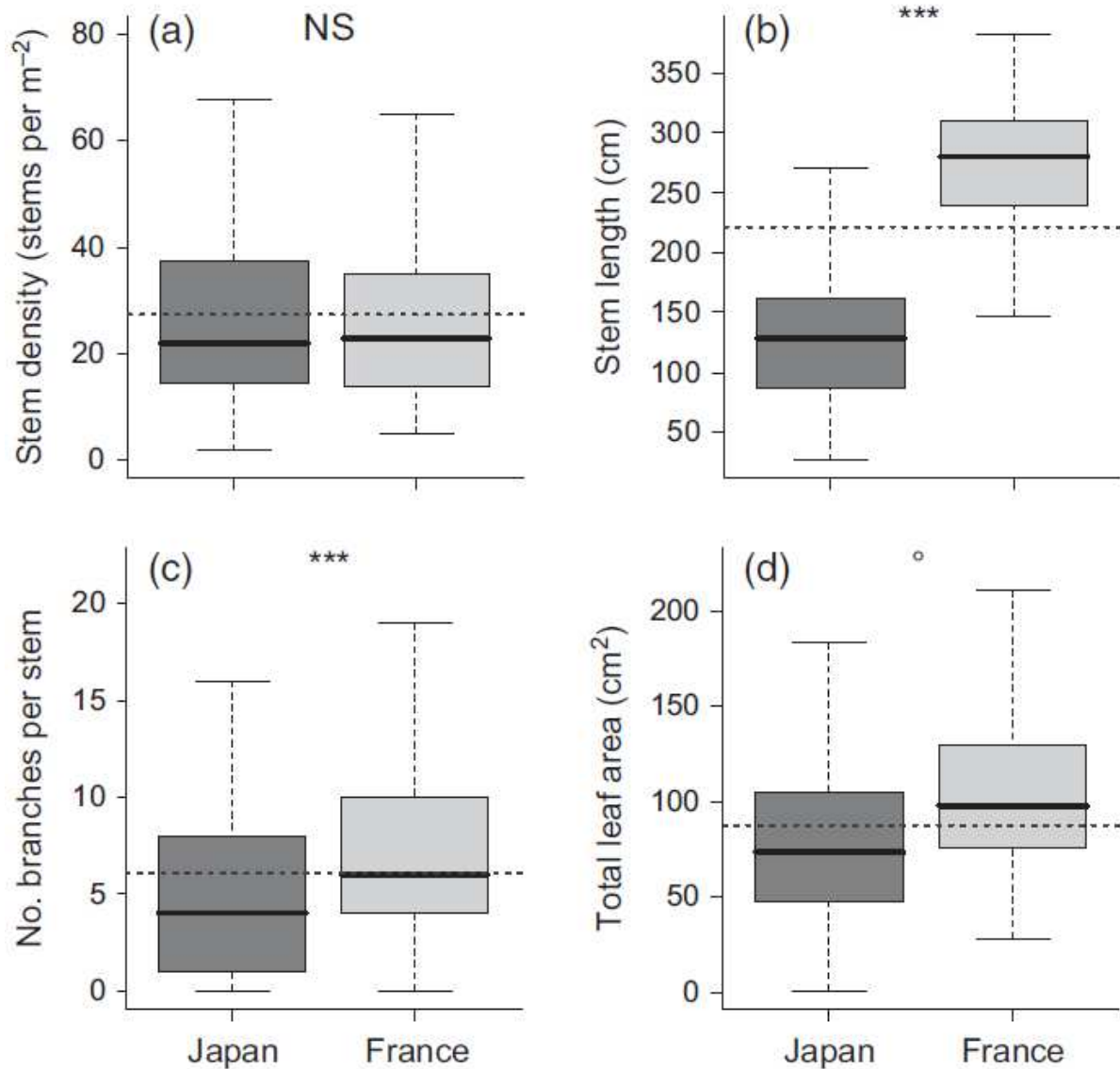
624 **Fig 3.** Plant growth. Stem density (a), stem length (b), number of branches per stem (c) and total leaf area (d) in

625 Japan and France. For each plot, the dotted line corresponds to the mean calculated on pooled data. Boxplots

626 display the median with first and third quartiles. Statistical results are shown (NS = non significant; ° = *P*-

627 value < 0.1; \*\*\* = *P*-value < 0.001).

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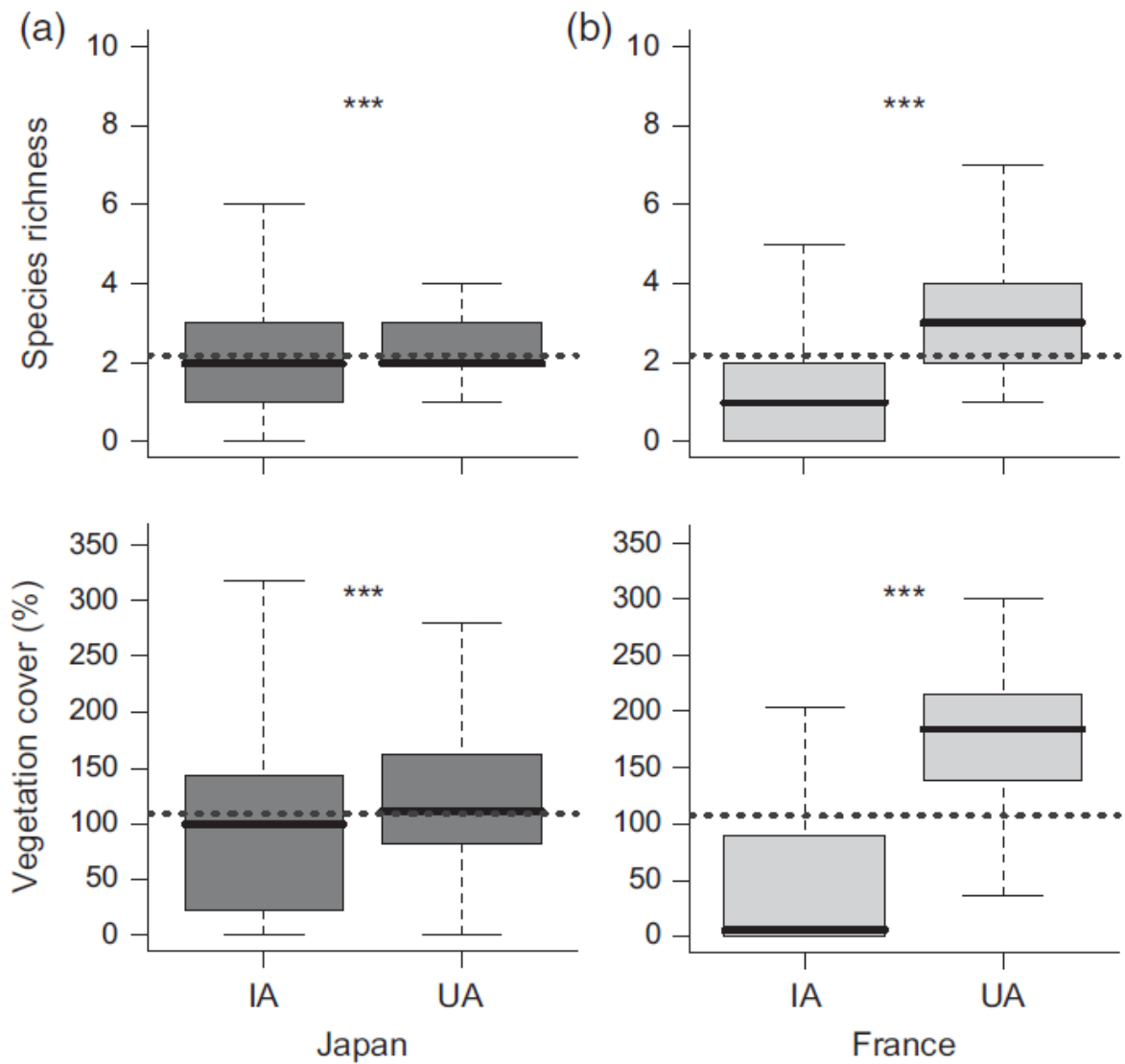
630 **Fig 4.** Within-site differences in floristic richness and vegetation cover of plant communities (*Fallopia japonica*

631 excluded) between invaded (IA) and uninvaded (UA) areas across ranges (Japan (A) and France (B)). For each

632 plot, the dotted line corresponds to the mean calculated on pooled data. Boxplots display the median with first

633 and third quartiles. Statistical results are shown (\*\*\*) =  $P$ -value < 0.001).

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**Fig 5.** 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.