

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

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

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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 Bruelheide 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.km², 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.km², 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⁻² vs. 112 inhabitants km⁻² 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 m² 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 m² 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 ± 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 ± 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 ± 1.99 stems m^{-2} ,
264 Fig. 3a and Table 2). On the contrary, stems were significantly taller (266.57 ± 6.02 vs. 133.38 ± 5.41 cm, Fig. 3b
265 and Table 2) and more ramified (8.00 ± 0.45 vs. 4.93 ± 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 ± 2.43 vs. 77.67 ± 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 ± 0.08 vs.
273 3.38 ± 0.11 species section $^{-1}$, $P = 0.028$), the same trend was statistically supported for vegetation cover
274 (122.88 ± 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

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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

Sampling site	Location	Latitude	Longitude	Elevation (a.s.l.)
JAPAN				
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
FRANCE				
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

600

601

602 **Table 2**

603

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

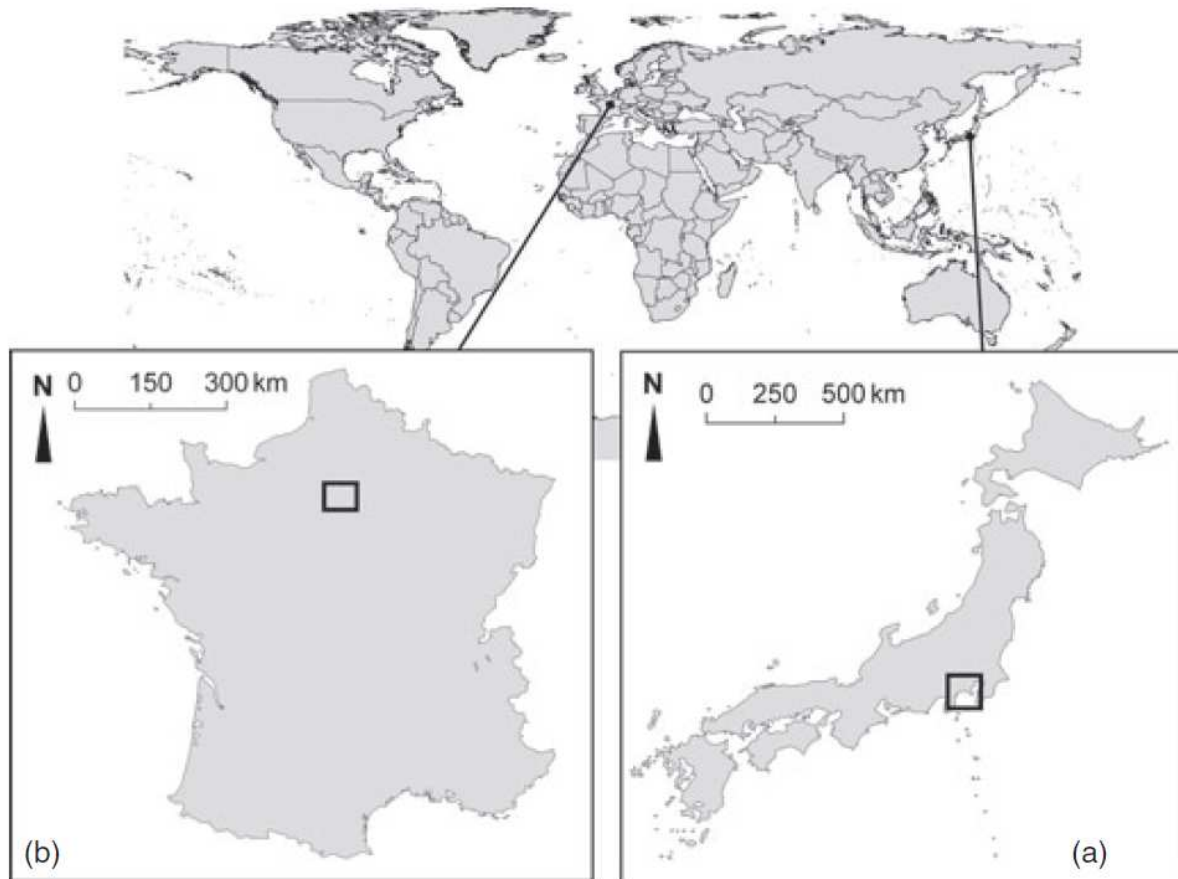
608

Variable	Factor	d.f.	F	<i>P</i>
<i>Herbivory</i>				
Proportion of damaged leaves	Range	18	130.593	<0.0001 ***
Leaf Area Loss (LAL)	Range	18	12.165	0.0033 **
<i>Plant growth</i>				
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 °
<i>Plant communities</i>				
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**

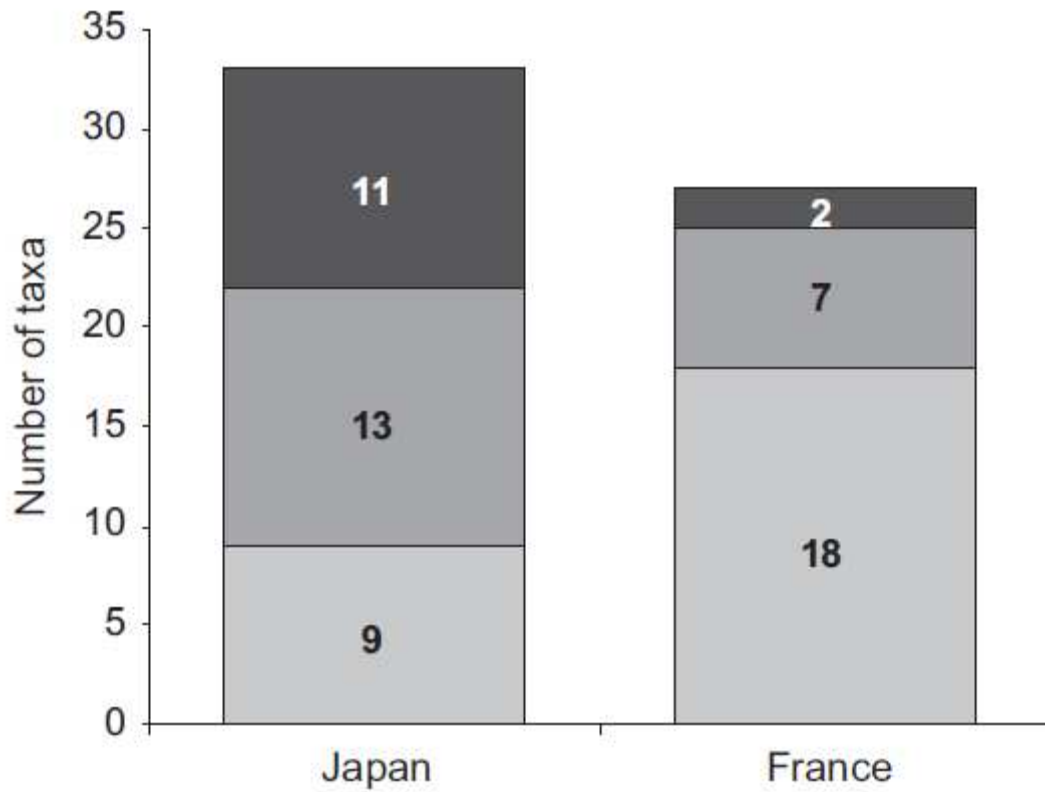


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613 **Fig 1.** Maps of the study areas. (A) Native range: Tokyo and Kanagawa prefectures, Japan; (B) Non-native
614 range: Greater Paris Area, France.

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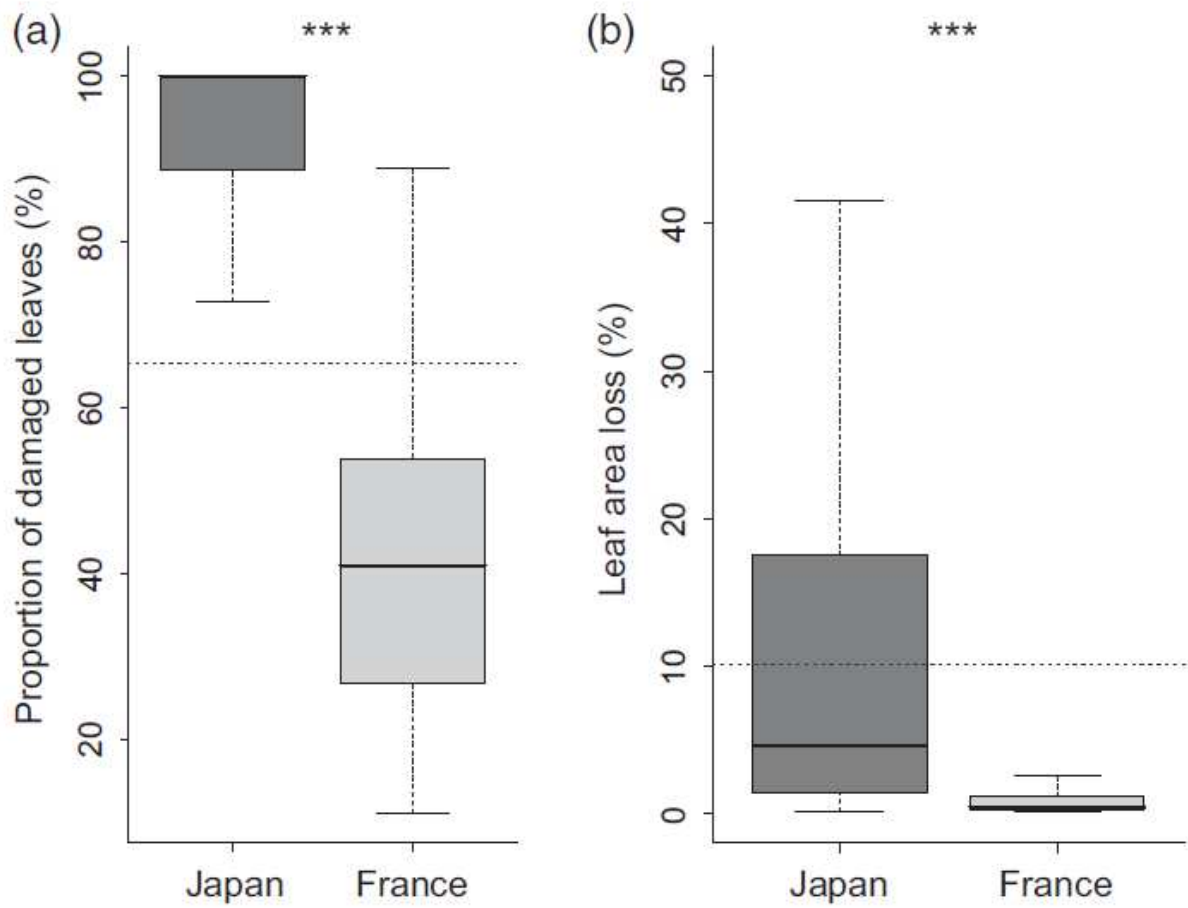
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618 **Fig 2.** Prevalence and severity of leaf damage. Proportion of damaged leaves (a) and leaf area loss (LAL, see
 619 Appendix S2) (b) expressed as percentages, in Japan and France. For each plot, the dotted line corresponds to the
 620 mean calculated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

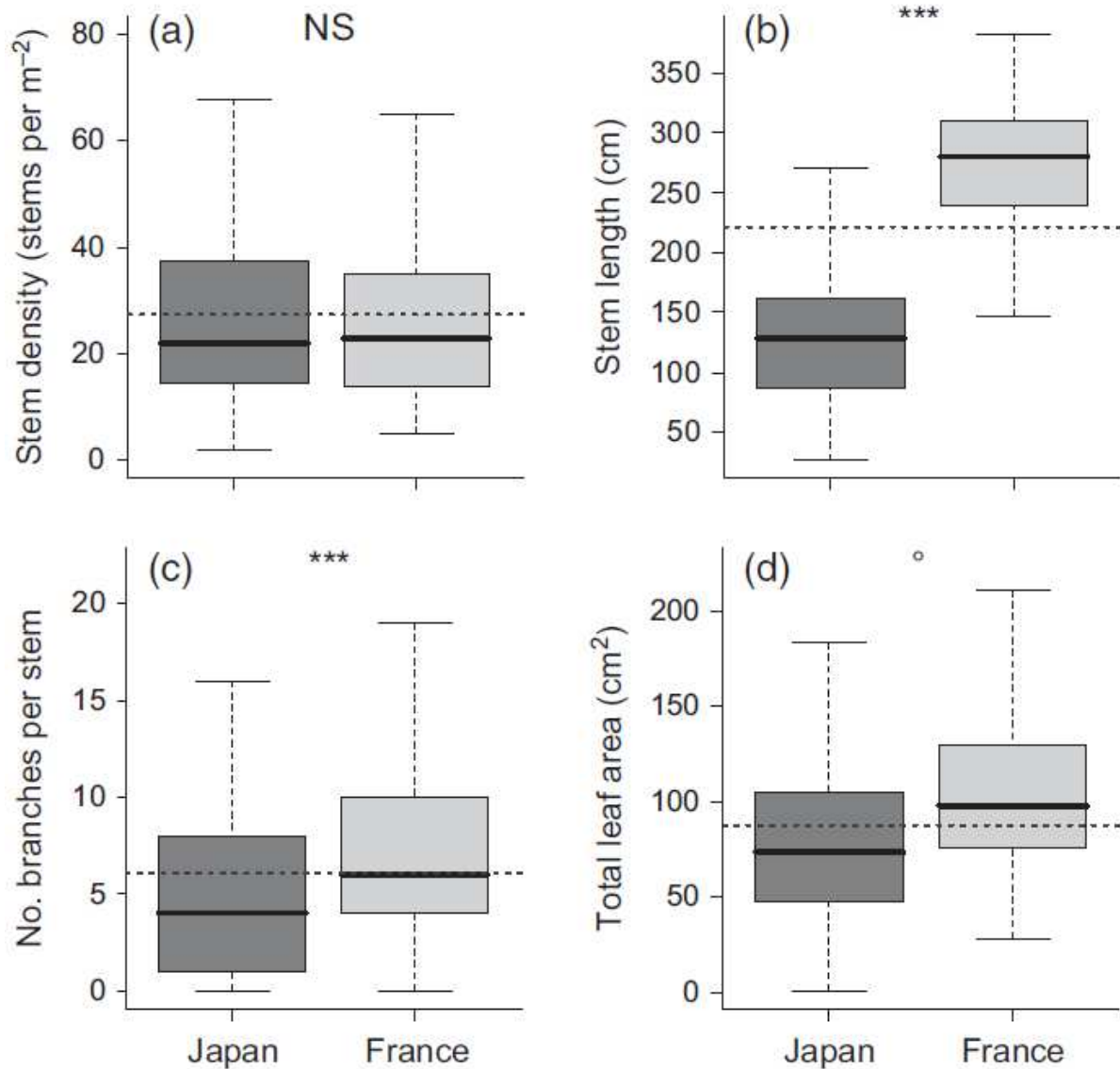
622



623

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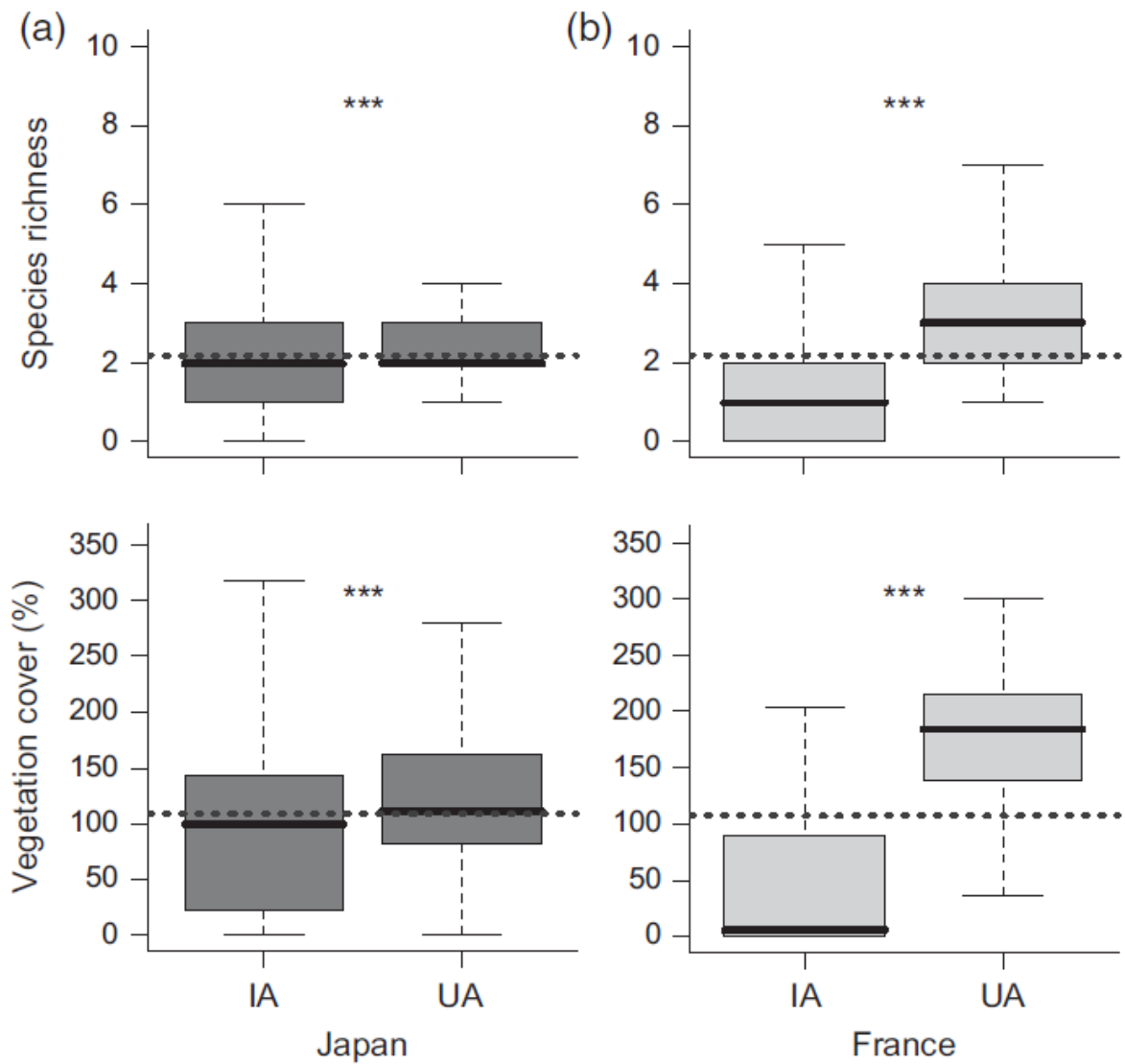
630 **Fig 4.** Within-site differences in floristic richness and vegetation cover of plant communities (*Fallopia japonica*

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.