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1 **Invasion by *Fallopia* spp. in a French upland region is related to anthropogenic disturbances**

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15 **Abstract** Within Europe, mountain ecosystems are generally less invaded by exotic plant species than are
16 lowland areas. This pattern is commonly attributed to climatic harshness, which limits invasive species presence,
17 and higher propagule pressure and rates of disturbance in lowlands, which favours dissemination. However, the
18 extent to which anthropogenic and natural disturbances contribute to invasive species presence in mountain and
19 lowland environments remains unclear. We conducted field observations in a lowland and an upland region in
20 France and measured environmental variables, estimated the natural and anthropogenic disturbance of plots
21 invaded by *Fallopia* spp. and compared them to non-invaded plots. Based on generalised linear mixed models,
22 the predictors of *Fallopia* spp. presence in the upland area only included anthropogenic elements such as the
23 presence of a road or trail and frequentation by humans, whereas both anthropogenic parameters and natural
24 components (light penetration, slope, and the presence of a watercourse) were retained as predictors for the
25 lowland region. We calculated the odds of *Fallopia* spp. presence for the increase of one unit of each predictor.
26 We conclude that the spread of *Fallopia* spp. in upland areas was mainly linked to human activity whereas
27 dissemination of the species occurred both through humans and in natural ways in lowland areas, and this may
28 be due to a more recent colonisation in the mountains. We therefore advise stakeholders to undertake actions in
29 mountain areas to specifically limit the dissemination of exotic species by humans and to monitor areas of high
30 invasion risk by exotic species, such as areas neighbouring trails and roads highly frequented by humans.

31 **Zusammenfassung**

32 In Europa werden Gebirgsökosysteme im Allgemeinen weniger stark von invasiven Pflanzenarten besiedelt als
33 tiefer gelegene Gebiete. Dieses Muster wird gemeinhin mit dem rauen Klima erklärt, das die invasiven Arten
34 limitiert, aber auch mit der höheren Einfuhr rate von Diasporen und der größeren Störungshäufigkeit in der
35 Ebene, was die Verbreitung fördert. Indessen ist unklar, in welchem Ausmaß anthropogene und natürliche
36 Störungen zum Auftreten von invasiven Arten in Berg- und Flachlandgebieten beitragen. Wir führten
37 Feldbeobachtungen in einer Berg- und einer Flachlandregion Frankreichs durch und maßen Umweltvariablen,
38 schätzten die natürliche und anthropogene Störung von Flächen, die von *Fallopia*-Arten besiedelt worden waren,
39 und verglichen diese mit unbesiedelten Flächen. Nach generalisierten linearen gemischten Modellen waren die
40 Faktoren, die das Auftreten von *Fallopia* im Bergland vorhersagten, allein anthropogene Landschaftselemente
41 wie Straßen und Wanderwege sowie die
42 Frequentierung durch Menschen, wohingegen sowohl die anthropogenen Parameter als auch natürliche Faktoren
43 (Lichteinfall, Hangneigung, Nähe von Fließgewässern) als Vorhersagefaktoren für das Flachland beibehalten
44 wurden. Wir berechneten die Wahrscheinlichkeit des Auftretens von *Fallopia* spp. für die Erhöhung um eine

45 Einheit für alle Vorhersagefaktoren. Wir schließen, dass die Verbreitung von *Fallopia* spp. im Bergland
46 hauptsächlich mit menschlichen Aktivitäten zusammenhing, während die Verbreitung der Arten im Flachland
47 sowohl durch den Menschen als auch auf natürliche Weise erfolgte. Dies könnte auf eine eher rezente
48 Besiedelung im Bergland zurückzuführen sein. Wir raten deshalb den Akteuren, im Bergland Maßnahmen zu
49 ergreifen, die speziell die Verbreitung exotischer Arten durch den Menschen begrenzen, und Gebiete mit hohem
50 Invasionsrisiko, wie Flächen entlang von stark von Menschen frequentierten Wanderwegen und Straßen zu
51 überwachen.

52

53 **Keywords:** invasibility, Japanese knotweeds *s.l.*, mountains, odds ratios, roads, watercourses

54

55

56 **Introduction**

57

58 The growing frequency of human exchanges is leading to the spread of more species' propagules worldwide.
59 Some exotic species become established and proliferate in their new range, leading in many cases to competition
60 with native species, to modifications of ecosystem functioning and to substantial losses in agricultural
61 production (Pyšek & Hulme 2005). Because of the impacts of invasive species, many management plans intend
62 to prevent further spread. However, data to assess the invasibility of some ecosystems is often lacking, which
63 hampers predictions of the future distribution of invasive species. For that purpose, key factors involved in the
64 invasion risk have to be identified. Knowledge of the current distribution, related to landscape or environmental
65 characteristics of invaded ecosystems, may help to identify these factors.

66 Invasion is the result of the interaction between propagule pressure, abiotic characteristics of the
67 invaded ecosystem, and biotic characteristics of the recipient community and the invading species. These drivers
68 fluctuate across space and time, and are likely to be influenced by humans (Catford, Jansson & Nilsson 2009).
69 Among abiotic factors, disturbance is noted as a key factor favouring the colonisation and establishment of
70 invasive species because it creates niche opportunities (Hobbs & Huenneke 1992), and sometimes dispersal
71 opportunities (for example during the construction of roads and buildings, Arévalo, Otto, Escudero, Fernández-
72 Lugo, Arteaga et al. 2010). Disturbance can be caused by natural events, such as floods and herbivory, or can be
73 anthropogenic, such as changes in land use, management and fertilisation (Lockwood, Hoopes & Marchetti
74 2007). In Europe, human population density and intensity of human activities appeared to well explain plant
75 invasions (Pyšek, Jarosik, Hulme, Kuhn, Wild et al. 2010), showing the great impact of anthropogenic
76 disturbances.

77 In temperate areas, it appears that invasive plant species richness is lower in mountain ecosystems than
78 in lowlands, but tends to increase (Pauchard, Kueffer, Dietz, Daehler, Alexander et al. 2009). It is not clear
79 whether this is a result of a time lag (stage of invasion), of reduced propagule pressure or of abiotic and biotic
80 conditions in mountains. Indeed, along altitudinal gradients, the relative importance of factors influencing
81 invasions is likely to change (Pauchard et al. 2009). For example, decreasing temperature constrains invasive
82 plant richness in elevated regions (Marini, Gaston, Prosser & Hulme 2009). The effects of disturbances are
83 uncertain, because anthropogenic disturbances, together with human population density, are assumed to decrease
84 with elevation, while natural physical disturbance, such as landslide or rock falls, are assumed to increase
85 (Pauchard et al. 2009). Moreover, it remains unclear whether the effects of both anthropogenic and natural

86 disturbances on the presence of invasive species are the same in mountain and lowland environments (Pauchard
87 et al. 2009). Thus, studies comparing links between disturbances and presence of invasive species in lowland and
88 upland sites are needed to clarify the role of disturbances in invasibility along an altitudinal gradient.

89 Japanese knotweeds *s.l.* (*Fallopia japonica* (Houtt.) Ronse Decraene (Japanese knotweed *s.s.*), *Fallopia*
90 *sachalinensis* (F. Schmidt ex Maxim.) Ronse Decraene and the hybrid *Fallopia x bohemica* (Chrték and
91 Chrtková); herein after referred to as *Fallopia* spp. or knotweed) are widespread invaders in North America
92 (Shaw & Seiger 2002) and Europe (Child & Wade 2000) where they are classified among the 20 most frequent
93 weeds (Lambdon, Pyšek, Basnou, Hejda, Arianoutsou et al. 2008). Large economic (Crowhurst 2006), faunistic
94 and floristic (Gerber, Krebs, Murrell, Moretti, Rocklin et al. 2008) impacts have been identified following its
95 invasion. Studying *Fallopia* spp. in the context of disturbances in elevated areas is interesting because they are
96 pioneer species, which regenerate easily from rhizomes and stem fragments (Bímová, Mandák & Pyšek 2003).
97 These plants generally occur in their invasive range in riparian habitats and in many types of anthropogenically
98 disturbed habitats, mainly along roads and railways (Bailey, Bímová & Mandák 2009). In addition, in elevated
99 areas, *Fallopia* spp. are not likely to be constrained by climate, as they seem to be cold tolerant (absolute
100 minimum temperature -30,2 °C, Beerling, Huntley & Bailey 1995).

101 In the present study, we focus on the importance of human and natural disturbances for the presence of
102 *Fallopia* spp. in lowland and upland sites. We hypothesize that *Fallopia* spp. presence is better explained by
103 disturbances than by environmental variables such as light availability above the plots, slope inclination and soil
104 granulometry (indicator of the capacity of the soil to retain water). We further postulate that in lowland areas
105 human disturbances (frequentation by humans, presence of working areas, roads and trails) increase the
106 probability of *Fallopia* spp. presence compared to natural disturbances (watercourses and erosion). In contrast,
107 we assume for upland areas that natural disturbances mainly influence *Fallopia* spp. presence.

108

109

110 **Materials and methods**

111

112 Study areas

113

114 The departments of Loire and Isere, two neighbouring departments situated in the southeastern part of France,
115 were the study areas. In the Loire department, crossed from south to north by the river Loire, which is highly

116 invaded by *Fallopia* spp., 29 sites were chosen by randomly generating four to six points at a distance of
117 approximately 10 km along six east-west transects (two transects in the northern region, two in the centre and
118 two in the southern part of the department). Starting from these points, the nearest physically accessible site
119 containing *Fallopia* spp. was surveyed in the field. When no invaded site was visible in the field, the nearest
120 invaded site listed in the botanical inventory by the National Botanical Conservatory of Massif Central was
121 surveyed. In the department of Isere, based on an inventory performed by the National Botanical Conservatory
122 of the Alps, 60 sites were recorded above an elevation of approximately 800 m (cf. <http://renouee.cemagref.fr>).
123 See Appendix A. for locations of studied sites.

124

125 Plot arrangement and variables measured

126

127 Each of the 89 sites included two paired plots (25 x 25 m each), one invaded by *Fallopia* spp. and the other non-
128 invaded. At each site, the centre of the *Fallopia* spp. patch and the plot centre were congruent. A non-invaded
129 plot was randomly chosen near the invaded plot; the centres of each plot were within a distance of 50 m (Fig.1).
130 Plots found to be infested within the surrounding plots were rejected and subsequently recorded as *Fallopia* spp.
131 infestations.

132 In the invaded plots, the total area occupied by *Fallopia* spp. was measured. The GPS coordinates and
133 elevation were recorded for both the invaded and non-invaded plots. The slope inclination was visually estimated
134 into four classes (none/low/intermediate/steep) and the slope aspect to the nearest 45° from north. Light
135 penetration in the plot was visually estimated to the nearest 10% by estimating the vertically projected cover of
136 the woody layer. The frequentation by humans at the site was visually assessed and recorded into three classes
137 (low, intermediate, high). Visible erosion was noted. The distance to the nearest tarred road, dirt track or trail,
138 watercourse and working area (including road works, settlements or timber stocking areas) were recorded in the
139 field when visible; otherwise, the distance was calculated using a GIS application. The maximal distance was
140 fixed at 9 999 m. Sampling occurred from August to September 2008 in both departments; in October 2009,
141 three additional sites were recorded in Isere.

142 Three soil cores (depth of 10 cm, diameter of 7 cm) were collected from each plot and pooled. The soil
143 samples were dried for 48 hours at 70 °C before fractionation into five classes: silt and clay (0-63 µm), sand (63
144 µm-2 mm), granules (2-4 mm), gravel (4-64 mm) and pebbles (>64 mm). Each fraction was weighted, and its
145 percentage of the total soil mass was calculated.

146

147 Data analysis

148

149 Based on the distance to roads, trails, watercourses, and working areas, the *Fallopia* spp. presence within a
150 radius of 10, 50, and 100 m for roads, trails, and watercourses and of 50 m for working areas was derived. Plots
151 in which a road, trail or working area were present within the above-mention radii were considered as “disturbed
152 by humans”, whereas plots in which soil erosion was visible or a watercourse was present were considered as
153 “naturally disturbed”.

154 The entire data set, containing 178 paired plots, was split into a lowland and an upland data set at an
155 elevation of approximately 900 m, corresponding to the limit between the collinean and the montane zones in the
156 region (Ozenda 1985). The lowland data set (number of plots N= 92) contained the paired plots for which the
157 invaded plot was situated below 895 m, and the other plots formed the upland data set (number of plots N= 86).
158 The significant differences between the lowland and upland sites were tested using the t-test for each variable.
159 Due to the topography of the two departments, the majority of lowland sites are situated in Loire and the
160 majority of upland sites are situated in Isere. However, because the departments are adjacent, have similar mean
161 temperatures and precipitations, and because we compared invaded plots and control plots within sites (GLMM
162 analyses), we are confident that the results are not flawed by the departments.

163 Three generalized linear mixed models (GLMMs) were calculated: a global model for the entire data set
164 and one model each for the upland and lowland data sets. The response variable *Fallopia* spp. presence and
165 absence were analysed using a logistic model, with logit as the link function, and with site as random factor. The
166 variables included in the analyses are shown in Table 1. Of the five soil classes, only the percentage of gravel
167 and the percentage of sand were retained in the analysis because the percentage of silt and clay and the
168 percentage of granules were highly correlated to the percentage of sand (Pearson correlation, for both $P < 0.001$;
169 correlation coefficient > 0.95). The percentage of pebbles was excluded from the analysis, as pebbles were only
170 present in 3.4% of all the soil samples. Forward selection was used to determine the best combination of
171 predictors for a minimal model.

172 For the entire data set and for each region, we analysed for each potential risk factor the conditions
173 under which the plots were invaded by *Fallopia* spp. relative to the non-invaded plots. The coefficient estimates
174 of each risk factor in the GLMM can be interpreted as the logarithm of the odds ratios of a plot containing
175 *Fallopia* spp. if the other predictors were constant (Quinn & Keough 2002). The “odds ratio” is the ratio of the

176 odds of a plot containing *Fallopia* spp. if exposed to one level of a risk factor relative to the odds of a plot not
177 containing *Fallopia* spp. if exposed to the next level of the same risk factor. Thus, an odds ratio of two for a
178 factor means that, for every increase in one unit of that risk factor, the odds of a plot containing *Fallopia* spp.
179 doubles. All the analyses were performed using R statistical language (R Development Core Team 2012).

180

181

182 **Results**

183

184 Differences between lowland and upland sites

185

186 The characteristics of the lowland and the upland plots, and the significance of the differences between the two
187 areas, are illustrated in Table 1.

188 The altitude of the lowest plot (in the lowland area) was 276 m, and the highest plot was elevated by 1665 m
189 (upland area). There was no significant difference between the area of the invaded plots of the lowland and of
190 the upland, although invaded plots of lowland (mean: 210 m²) tended to be larger (mean in upland: 109 m²,
191 Table 1).

192 At all sites (control and invaded), light penetration was lower in the upland plots, leading to more shading on the
193 plots. The slope inclination was higher in lowland sites. The analysis of soil granulometry showed that upland
194 plots were slightly richer in soil pebble (Table 1).

195 The most striking differences were found concerning the human impact near the plots. In the upland region, the
196 invaded plots and their paired control sites were situated in closer vicinity to working areas and trails compared
197 to plots in the lowland area (Table 1), indicating the importance of human disturbance for the colonisation of the
198 upland region by knotweed. In contrast, the lowland and upland sites showed no significant differences in
199 estimated frequentation or distance to nearest road (Table 1).

200 Lowland and upland plots showed no significant differences concerning natural disturbances. All plots were
201 situated near a watercourse, and the distance to the nearest watercourse and the frequency of eroded zones did
202 not significantly differ (Table1).

203

204 Factors influencing the presence of knotweeds

205

206 In the global analysis which considered sites in both, the upland and lowland regions, the predictors of *Fallopia*
207 spp. presence belonged to three classes: environmental variables (light penetration), natural disturbance
208 (presence of a watercourse), and human disturbance (frequentation by humans, presence of a road or trail).
209 However, analysing the upland and lowland sites separately led to different predictors of knotweed presence for
210 both regions (Table 2). Only anthropogenic elements, such as the presence of a road or a trail within a radius of
211 10 m and the frequentation by humans in the surroundings of the plot, were retained in the reduced GLMM for
212 the upland region while for the lowland region both anthropogenic and natural components, such as light
213 penetration, slope inclination, and the presence of a watercourse within a radius of 10 m, were retained as
214 predictors.

215

216 Factors increasing the odds of a plot containing knotweeds

217

218 In the global analysis that included all sites, the odds of a plot containing *Fallopia* spp. increased with increasing
219 light penetration, with the presence of a road, a trail or a watercourse, and with a high frequentation by humans
220 (Table 3). For the upland plots, a shift from low frequentation to intermediate or similarly from intermediate to
221 high frequentation by humans increased more than four times the probability of encountering knotweeds.
222 Frequentation by humans represented the factor with the highest leverage, while the presence of a trail in the plot
223 vicinity nearly doubled, and the presence of a road increased the same probability by about 50% (Table 3). For
224 the lowland plots, the presence of a river within 10 m and the presence of a road more than doubled the odds of a
225 plot containing knotweeds. However, increasing slope inclination from low to intermediate augmented by about
226 8 the odds ratio and by about 11 when intermediate slopes became steep ones, but these numbers have to be
227 interpreted with caution as their variability, indicated by the large range of the confidence interval, is high.
228 Compared to these high odds, increasing light availability by 10% had hardly any effect on *Fallopia* presence
229 (Table 3) even when light availability was retained as a significant factor in the GLMM (Table 2).

230

231

232 **Discussion**

233

234 Factors influencing *Fallopia* spp. presence

235

236 Species belonging to the genus *Fallopia* spp. are supposed to greatly benefit from disturbance outside their
237 native range because of their high colonisation potential, allowing them to dominate such areas rapidly (Tiébré,
238 Saad & Mahy 2008). In accordance with our first hypothesis, the presence of *Fallopia* spp. is, to a large extent,
239 explained in this study by disturbances of both natural (watercourse) and human (trails, roads, frequentation)
240 origin. Close associations between knotweeds and human disturbance along rail or road infrastructures (Bímová,
241 Mandák & Kašparová 2004, Tiébré et al. 2008) and knotweed and naturally disturbed watercourses (Beerling
242 1991) have been reported. Road infrastructures may serve as vectors of alien species dispersal (Arévalo et al.
243 2010, Coffin 2007); similarly, watercourses may contribute to the dispersal of alien propagules (Richardson,
244 Holmes, Esler, Galatowitsch, Stromberg et al. 2007) and, in particular, of knotweed achenes (Rouified, Puijalon,
245 Viricel & Piola 2011). Moreover, the hydraulic dynamics of watercourses, which lead to temporarily reduced
246 competition for space and high resource availability on banks, make those sites important habitats for alien
247 species (Richardson et al. 2007).

248 Our study compared two disturbance types that influence the presence of *Fallopia* spp. at different
249 elevations. Although the global analysis, including all the low- and upland sites, indicated both human and
250 natural disturbances as predominant, the separate analyses clearly suggested different predictors for knotweed
251 presence at the two levels of elevation. Contrary to our hypothesis, natural disturbance and its associated factors
252 did not explain the presence of *Fallopia* spp. in the upland areas, confirming that it is difficult to predict what
253 type of disturbance will be predominant based on the elevation of the area (Pauchard et al. 2009). Indeed, several
254 studies highlight the importance of anthropogenic disturbance in explaining plant invasions in mountains
255 (Alexander, Naylor, Poll, Edwards & Dietz 2009, Arévalo et al. 2010).

256 The pattern of our results is consistent with the directional ecological filtering hypothesis (Alexander,
257 Kueffer, Daehler, Edwards, Pauchard et al. 2011), which states that the colonisation of mountains by non-native
258 species is the result of the dispersal from lowland sources of species with wide elevational amplitude.
259 Directional ecological filtering implies firstly that species reaching higher elevations are good dispersers and
260 secondly that these species must also have wide climatic tolerance because they are able to establish populations
261 across the full elevational gradient (Alexander et al. 2011). The case of *Fallopia* spp. fits these assumptions.
262 First, they are able to efficiently disperse both asexually and sexually (Bailey et al. 2009). In our study, roads
263 and trails explained the presence of the species and may be more important dispersal pathways than sites of
264 niche opportunities: rhizome fragments of *Fallopia* spp. could easily be dispersed through soil transport and
265 engine circulation during construction works and possibly by foot-traffic dispersing stem fragments and seeds.

266 Second, *Fallopia* spp. have wide climatic tolerance: *Fallopia japonica* can resist cold temperatures up to a
267 minimum threshold estimated between -32.0 and -25.8 °C (Beerling et al. 1995). Although we did not measure
268 the temperatures or other climatic variables in upland and lowland regions, we assume that the pattern of the
269 presence of the species would not be influenced by the different climates because of their wide climate tolerance,
270 which is corroborated by the presence of *Fallopia* spp. up to 1600 m asl.

271 In contrast to the upland region, where solely anthropogenic disturbances factors explained the presence
272 of knotweeds, both human disturbances, natural disturbances, and other environmental factors such as light
273 penetration and slope inclination were important in the lowland region. We deduce from greater variety of the
274 predictive factors that the invasion process of *Fallopia* spp. is older at low elevation. In the lowland, the spread
275 of *Fallopia* spp. appeared to be under “natural” regulation and no longer only linked to human presence:
276 knotweeds may have reached the stage of propagation in the landscape (stages *sensu* Theoharides & Dukes
277 2007), whereas the invasion process appeared not to have exceeded the stages of colonisation or establishment in
278 the mountainous regions. In the latter spread is perhaps beginning, related to anthropogenic disturbances, as
279 vectors of niche opportunities and propagules’ dispersers.

280 The influence of light penetration and slope inclination in the lowland region can be interpreted as
281 another evidence of natural dispersal: *Fallopia* spp. is favoured on sites with a high disturbance rate, as steep
282 slopes are mainly found along rivers with high erosion activity, and with high light availability, indicating less
283 tree and shrub cover to shade *Fallopia* spp. stands. Indeed, knotweeds are pioneer species in their native range,
284 colonising sites with a high light availability (Adachi, Terashima & Takahashi 1996) and rarely dominate in their
285 exotic range in mature forests, which filter a significant portion of photons (McClain, Holl & Wood 2011). Light
286 availability, therefore, appears to be one of the factors that might directly affect the frequency and the cover of
287 exotic species (McClain et al. 2011; Dommanget, Spiegelberger, Cavaillé & Evette 2013) which is confirmed by
288 our findings. Consequently, succession that shifts the understory from light-demanding to shade-tolerant species
289 may limit colonisation by invasive species (McClain et al. 2011).

290 Our study did not allow a distinction between light availability as the cause or consequence of *Fallopia*
291 spp. presence. One may interpret the higher light availability at invaded sites as the consequence of a process of
292 competitive exclusion induced by knotweed, leading to a lower cover of trees and shrubs and, consequently, a
293 higher light penetration. However, as described above, it may also be that knotweeds in particular invade sites
294 with high light availability (no or only low tree/shrub cover), which may be interpreted as the result of a
295 disturbance or as an earlier successional stage that is more prone to invasion (Rejmánek 1989). In our study, the

296 odds of *Fallopia* presence with an increase of 10% of light availability were low, which may seem inconsistent
297 with the high influence of light in models explaining the presence of the plant. A connection between
298 disturbances and light may explain this paradox.

299 To conclude, our study clearly shows the link between human activities and the presence of *Fallopia*
300 spp. in a mountainous region, contrary to a lowland region where biotic variables and natural disturbance are
301 involved. Future studies are necessary to precise the relative importance of time, as different kinds of
302 disturbances may be involved at different stages of the invasion process, and of abiotic factors, such as nutrient
303 composition and hydraulic variables, which may differ in lowland and upland regions.

304

305 Invasion risk and advice to stakeholders

306

307 The results of our study indicate that (i) natural or anthropogenic disturbance plays a key role in explaining the
308 presence of *Fallopia* spp. and (2) the importance of the origin of the disturbance differs at low and high
309 elevations. In light of this, we recommend surveying of steep river banks next to roads in lowland regions and
310 highly frequented sites neighbouring roads and trails above 900 m where invasion risk by *Fallopia* spp. is high.
311 European mountains are one of the few ecosystems where a proactive management strategy is still possible
312 (McDougall, Khuroo, Loope, Parks, Pauchard et al. 2011). Early detection surveys in such zones as those
313 described above where invasion risk is high and the elimination of a few individuals when eradication is still
314 possible are most likely more cost effective than attempts of eradication or control once invasion has occurred
315 (Wittenberg & Cook 2001).

316

317

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319

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326 Appendix A. Supplementary data

327 Supplementary data associated with this article can be found, in the online version, at

328

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330

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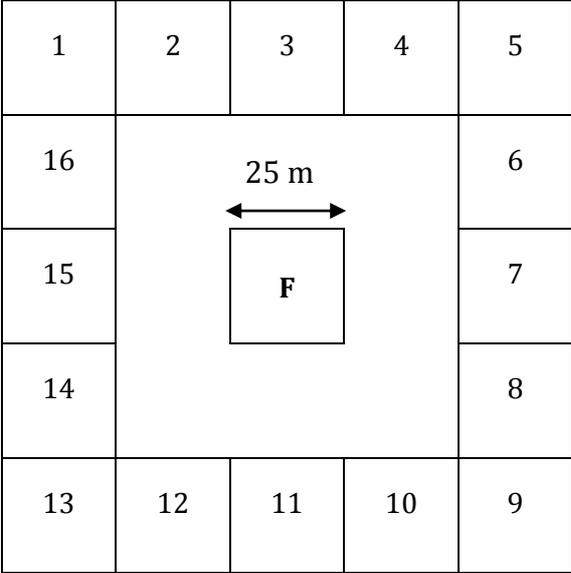
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419 **Fig. 1.** Schematic representation of invaded and control plots location in one site.
420 F represents the invaded plot. Associated control plot was randomly chosen among the 16 areas defined around
421 the invaded plot. Measurements were carried out in a 25x25 metres square in both plots.



1 **Table 1.** Area of the *Fallopia* spp. plots, elevation and variables included in the analysis measured at lowland and upland sites, in control and invaded plots (mean and
 2 standard error). The P-values indicate the significance of t-tests between the lowland and upland sites (control and invaded plots are considered together).
 3
 4

Variable	Unit	Lowland				Upland				Lowland vs Upland P value
		Control		Invaded		Control		Invaded		
		Mean	SE	Mean	SE	Mean	SE	Mean	SE	
Area of invaded plots	Square metres	-	-	210.5	53.5	-	-	109.3	22.6	0.087
Elevation	Metres	630	35	629	34	1049	29	1050	29	<0.001
Environment										
Slope inclination	Flat(0)/low(1)/intermediate(2)/steep(3)	1.3	0.2	1.8	0.2	1.3	0.2	1.3	0.2	0.034
Light penetration	Percentage	59.2	5.7	62.3	5.0	27.2	5.1	27.6	3.7	<0.001
Soil pebbles	Proportion	0.53	0.03	0.52	0.03	0.60	0.04	0.60	0.03	0.047
Soil granules	Proportion	0.14	0.01	0.15	0.01	0.12	0.01	0.13	0.01	0.260
Soil sand	Proportion	0.32	0.03	0.33	0.03	0.28	0.03	0.26	0.02	0.066
Human disturbance										
Human disturbance	Presence(1)/Absence(-1)	0.4	0.1	0.6	0.1	0.9	0.1	0.9	0.1	0.009
Frequentation	Low(-1), intermediate(0), high(1)	-0.1	0.1	0.5	0.1	-0.3	0.1	0.1	0.1	0.688
Working area	Presence(1)/Absence(-1)	0.1	0.1	-0.1	0.1	0.6	0.1	0.7	0.1	<0.001
Distance to the nearest working area	Metres	5659	738	5224	743	2093	628	1628	570	<0.001
Working area within 50 m	Presence(1)/Absence(-1)	-0.2	0.1	-0.1	0.1	0.6	0.1	0.7	0.1	<0.001
Road	Presence(1)/Absence(-1)	1.0	0.1	1.0	0.1	1	0	1	0	0.323
Distance to the nearest road	Metres	25.8	4.8	14.7	4.1	21.0	4.6	13.5	3.8	0.823
Road within 10 m	Presence(1)/Absence(-1)	-0.3	0.1	0.3	0.1	0.1	0.1	0.4	0.1	0.490
Road within 50 m	Presence(1)/Absence(-1)	0.8	0.1	0.9	0.1	0.7	0.1	0.8	0.1	0.410

Road within 100 m	Presence(1)/Absence(-1)	0.9	0.1	0.9	0.1	0.9	0.1	1	0	0.160
Trail	Presence(1)/Absence(-1)	0.1	0.1	-0.1	0.1	-0.5	0.1	-0.4	0.1	0.084
Distance to the nearest trail	Metres	2466	630	2462	630	321	231	309	231	0.002
Trail within 10 m	Presence(1)/Absence(-1)	-0.6	0.1	-0.2	0.1	-0.7	0.1	-0.4	0.1	0.362
Trail within 50 m	Presence(1)/Absence(-1)	-0.2	0.1	-0.1	0.1	-0.3	0.1	0.2	0.1	0.777
Trail within 100 m	Presence(1)/Absence(-1)	-0.1	0.1	0.1	0.1	0.2	0.1	0.3	0.1	0.220
Natural disturbance										
Natural disturbance	Presence(1)/Absence(-1)	-0.6	0.1	-0.2	0.1	-0.5	0.1	-0.8	0.1	0.281
Watercourse	Presence(1)/Absence(-1)	1	0	1	0	1	0	1	0	0.999
Distance to the nearest										
watercourse	Metres	1170	460	1165	460	371	230	366	231	0.126
Watercourse within 10 m	Presence(1)/Absence(-1)	-0.8	0.1	-0.4	0.1	-0.7	0.1	-0.5	0.1	0.594
Watercourse within 50 m	Presence(1)/Absence(-1)	0.1	0.1	0.1	0.1	-0.2	0.1	-0.1	0.1	0.344
Watercourse within 100 m	Presence(1)/Absence(-1)	0.4	0.1	0.3	0.1	0.1	0.1	0.2	0.1	0.641
Erosion	Presence(1)/Absence(-1)	-0.8	0.1	-0.7	0.1	-0.8	0.1	-0.9	0.1	0.344

1 **Table 2.** Factors influencing the presence of *Fallopia* spp. in an upland region of France, a lowland region and in
 2 all sites (GLMM analysis). Df: degrees of freedom. χ : Chi-value. P: P-value. The asterisks indicate the degree of
 3 significance: °P < 0.1, *P < 0.05, **P < 0.01, ***P < 0.001

4

	All Sites			Upland			Lowland		
	Df	χ	P	Df	χ	P	Df	χ	P
Presence of a watercourse within 10 m	1	4,1	0,043 *			-----	1	5,3	0,021 *
Presence of a road within 10 m	1	11,0	< 0,001 ***	1	3,7	0,055 °	1	8,6	0,003 **
Presence of a trail within 10 m	1	3,9	0,050 *	1	4,2	0,040 *			-----
Frequentation	2	11,6	0,003 **	2	8,4	0,015 **	2	5,1	0,078 °
Light penetration	1	4,3	0,039 *			-----	1	10,5	0,001 **
Slope inclination			-----			-----	3	9,5	0,023 **
Residuals	171			81			83		

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1 **Table 3.** Odds-ratios for factors influencing the odds to find a plot containing *Fallopia* spp. for all sites, lowland
 2 sites and upland sites (95% confidence intervals are indicated in parentheses).

3

	Sites		
	All	Upland	Lowland
Presence of a watercourse within 10 m	1.57 (1.01-2.44)	---	2.67 (1.16-6.16)
Presence of a road within 10 m	1.77 (1.26-2.47)	1.62 (0.99-2.64)	2.29 (1.32-3.96)
Presence of a trail within 10 m	1.53 (1.00-2.35)	1.91 (1.03-3.53)	---
Shifting from no frequentation to low frequentation	3.38 (1.53-7.47)	4.76 (1.52-14.90)	4.28 (1.03-17.78)
Shifting from low to intermediate frequentation	3.92 (1.60-9.64)	4.37 (1.27-15.09)	5.66 (1.12-28.62)
Increase of 10% light penetration	1.01 (1.00-1.03)	---	1.04 (1.02-1.06)
Shifting from no slope to low slope	---	---	4.07 (0.78-21.20)
Shifting from low to intermediate slope	---	---	8.49 (1.72-41.87)
Shifting from intermediate to steep slope	---	---	11.68 (2.14-63.71)

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Appendix A. Map of recorded sites in Loire and Isère departments.

