Reconsidering interspecific co-occurrence of native and invasive plants in an anthropogenic riparian ecosystem

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Abstract

Invasive non-native plants are considered mostly though negative interactions, but are increasingly recognized as potential contributors to ecosystem functioning. By modifying microhabitats, resource availability and species interactions, non-natives plants may reshape and maintain the living conditions of native plant communities. We conducted an observational field study to quantify the interspecific relationships of coexistence between riparian herbaceous plants and three vegetation types: *Fallopia* x *bohemica* (invasive non-native), *Rubus caesius* (invasive native), and an uninvaded riparian forest (control). Seasonal monitoring of species richness was carried out over one year, combined with measurements of vegetation cover rate and functional traits relating to growth, flowering, and seed production in spring. *Fallopia* patches showed similar species richness, vegetation cover and functional traits compared to uninvaded areas in spring. In contrast, *Rubus* was associated with a lower number of co-occurring species and a reduction of growth and reproduction. Our findings demonstrate that *Fallopia* was associated with comparable plant richness and measured spring trait values under the uninvaded areas, and to a greater extent than *Rubus*. Rather than viewing non-native plants solely as threats, our example highlights the importance of adopting a more nuanced, context-dependent perspective that considers their potential to help maintain biodiversity in ecosystems subject to anthropogenic alterations.

KEYWORDS

Anthropogenic riparian ecosystem, biodiversity, biological invasion, species coexistence, *Fallopia* x *bohemica*, functional traits, phenology, *Rubus caesius*

INTRODUCTION

In ecology, species interactions have traditionally been characterized by conflict, even though positive interactions are now recognized as a concept that contributes to species coexistence (Bruno et al. 2003, Losapio 2023). Competition and predation are considered to be the key factors that shape community structure (Chesson 2000, MacDougall et al. 2009, Bartomeus and Godoy 2018). Especially for plants, where competition for resources has long been identified as a major driver of species coexistence (Tilman 1994). According to the principle of competitive exclusion (Grinnell 1904), two species cannot coexist when they compete for a single limiting resource (Chesson 2000, Bartomeus and Godoy 2018). However, positive interactions can also play an important role in structuring communities and promoting coexistence (Rodriguez 2006, Angelini et al. 2015). Facilitative interactions among neighboring species may increase individual fitness and population growth, thereby influencing species diversity and community dynamics (Bruno et al. 2003, Losapio 2023). For example, *nurse plants* can improve microhabitat conditions for other plant species by lowering temperature, increasing humidity, or enhancing soil fertility, which can facilitate seedling establishment (Odling-Smee et al. 1996, Badano et al. 2016). Moreover, phenological coexistence provides temporal differentiation that facilitates coexistence (Westoby et al. 2002, Adler et al. 2014, Cleland and Wolkovich 2024). Differences in vegetative phenology (i.e., the timing of key growth and reproductive stages) enables species to share similar resources while occupying distinct temporal niches. For instance, plants with minimal phenological overlap can optimize their life cycles at different times of the year, thereby promoting community-level coexistence (Cleland and Wolkovich 2024).

Positive interaction such as facilitation emerges as a significant force shaping ecosystems, especially in constrain conditions where organisms are increasingly exposed to rapid biotic

and abiotic disturbances caused by human activities (Callaway and Walker 1997, Schlaepfer et al. 2011, Badano et al. 2016, De Bello et al. 2021). In these circumstances, positive interactions can promote species coexistence when certain plants stabilize environmental conditions within microhabitats (Bruno et al. 2003, Oliver et al. 2015, De Bello et al. 2021). Major anthropogenic pressures include habitat destruction, intensive chemical use, and the overexploitation of natural resources, leading to a loss of ecological functions (Blondel 2008). As these changes intensify, species that are tolerant to disturbed environments, such as invasive non-native species, are becoming more prevalent (Lembrechts et al. 2016). While much of the literature focuses on the antagonistic interactions of these non-native taxa, a few studies also recognize their potential beneficial impacts on perturbed ecosystems (Rodriguez 2006, Angelini et al. 2015, Ramus et al. 2017, Vimercati et al. 2020, Lee et al. 2024). As passengers of anthropogenic disturbances, non-native species can exploit newly formed or vacant niches (Shea 2002, MacDougall and Turkington 2005, Hobbs et al. 2009, Thomsen and Wernberg 2015). The field of conciliation biology recognizes that such species can perform valuable ecological functions, providing resources and creating refuges in inhospitable environments (Carroll 2011, Schlaepfer et al. 2011, Badano et al. 2016, Cassini 2020). These often overlooked functional roles can contribute to conservation goals by mitigating biodiversity decline and strengthening the resilience of degraded ecosystems (Rodriguez 2006, Goodenough 2010, Oliver et al. 2015, Tassin et al. 2017, De Bello et al. 2021).

In this study, we used a comparative approach to investigate the coexistence dynamics of two invasive plant taxa: *Fallopia* x *bohemica* (non-native, hereinafter *Fallopia*) and *Rubus caesius* (native, hereinafter *Rubus*). Both species are disturbance-tolerant pioneers that form dense clonal patches and actively colonize degraded European riparian ecosystems (Tokarska-Guzik et al. 2006, Tiébré et al. 2008, Rouifed et al. 2014, Thiébaut et al. 2020). These hydrosystems

are heavily impacted by urbanization, intensive agriculture, dam construction, water extraction and climate change (Nilsson et al. 2005, Palmer et al. 2009). The categorization of these two taxa is still influenced by their biogeographic origin. *Fallopia*, being non-native, has long been the target of management programs due to its perceived threat to biodiversity, whereas *Rubus* is generally regarded as playing a functional role in ecosystems (Schnitzler and Muller 1998, Bottollier-Curtet et al. 2011, Cottet et al. 2018, 2020). However, the negative impacts of *Fallopia* may be overstated, at least in anthropogenically modified ecosystems, and recent studies suggest its potential contributions to hydrosystem functioning (Lavoie 2017). Although *Fallopia* patches are often associated with competitive exclusion, they can provide physical structure and nutritional resources for insect communities (Gippet et al. 2018, Cucu et al. 2024) and facilitate the establishment of early-season plant species through stem senescence during winter and increased light availability in spring (Tokarska-Guzik et al. 2006, Matysiak 2021). *Fallopia* patches can also create nitrogen-rich niche, increasing soil nitrogen availability for others plants species (Tateno and Hirose 1987, Dassonville et al. 2011, Bardon et al. 2014, Cantarel et al. 2020, Béraud et al. 2024). Furthermore, leaf litter decomposition in riparian *Fallopia* patches does not inhibit plants establishment and may even promote facilitative interactions, whereas *Rubus* often has inhibitory effects (Staentzel et al. 2020). Nonetheless, current research works remains biased toward the study of negative effects, reinforcing a demonized subjective perception of non-native species (Vimercati et al., 2020; Sagoff, 2018; Larson et al., 2005; Correa et al., 2020).

In order to assess the interspecific coexistence relationships between native and non-native riparian species, we examined the occurrence and performance of herbaceous flora within clonal patches of *Fallopia* and *Rubus*. We hypothesize that *Fallopia*, through its functional strategies (ability to create a nitrogen niche and distinctive stem phenology), supports plant coexistence at levels comparable to uninvaded areas (H1) and promotes higher growth- and

reproduction-related trait values compared to the native invasive *Rubus* (H2). To test these hypotheses, we conducted observational field surveys in an anthropogenic riparian ecosystem, where invaded and control areas consisting of an uninvaded riparian forest were monitored seasonally. Over one year, we monitored herbaceous species richness and abundance for each season, and measured functional traits related to growth and reproduction in spring. By comparing plant-community associations across native and non-native vegetation types, this study examines how species identity and local environmental context may shape riparian plant communities in human-modified landscapes.

MATERIALS AND METHODS

Study system and sampling design

The study was conducted in the riparian habitats of the Ain River in France (Figure 1). With a catchment area of 3,630 km², the gravel bar river flows from the Jura Mountains to the Rhône River (Judes et al. 2023). The mean annual temperature ranges from 5°C to 15°C, and the mean annual precipitation ranges from 750 mm to 1000 mm. Since the 20th century, the river has been subject to numerous anthropogenic disturbances. The hydrological regime and sediment dynamics have been altered by a chain of six hydroelectric dams and a nuclear power plant located along the river (Judes et al. 2023). Intensive agricultural lands and transport infrastructures are located within the floodplain, close to the riparian forest (Godfroy et al. 2023). In addition, tourist activities such as kayaking, fishing and hiking attract large numbers of visitors throughout the year. These activities lead to regular maintenance operations on the river's active channel, resulting in sedimentary restructuring that favor the establishment of pioneer species, such as invasive non-native plants.

Four sites were selected for sampling and studied in 2025, a year without exceptional ecological or hydrological event (Figure 1). They were distributed along a 12 km stretch, at an altitude of 200 m, and at a maximum distance of 15 m from the river (Site 1 - 45.964865, 5.255974 | Site 2 - 45.964234, 5.256924 | Site 3 - 45.88799, 5.237945 | Site 4 - 45.857698, 5.22896). All banks were considered biologically comparable and were subjected to the same environmental and anthropogenic disturbances. Vegetation was composed of riparian herbaceous plants, shrubs and trees (such as poplar, ash, willow and maples species - *Populus nigra*, *Fraxinus excelsior*, *Salix alba*, *Acer platanoides*), and substrates were composed of sediment, soil and pebbles.

In each site, we identified three vegetation types in the riparian forest (Figure 1): an understory dominated by a clonal invasive non-native species (knotweeds - *Fallopia* x *bohemica* (Chrtek & Chrtková) J. P. Bailey, named *Fallopia* and designated F), an understory dominated by a clonal invasive native species (brambles – *Rubus caesius* L., named *Rubus* and designated R), and an uninvaded understory (uninvaded riparian forest - control designated C). Both non-native and native species were widespread along the river under the forest canopy, installed for at least ten years, and forming dense clonal patches side by side that facilitated sampling boundaries. Each vegetation type covered an area of approximately 100 m² and was divided into three equal plots (3 x 3 m) to identified native species.

Seasonal botanical surveys

Seasonal vegetation surveys were conducted during one year to assess the effect of both native and non-native species on the herbaceous species composition and phenology. Sites were visited in winter (January), spring (April), summer (July) and autumn (October). For each vegetation type and within each plot (Figure 1), all herbaceous species were recorded,

144 with *Fallopia* and *Rubus* also included in the survey. Only grasses have not been identified to
145 species level, due to very early stages of grow in spring (*Poaceae* spp.). *Fallopia* produces
146 new stems and large leaves in spring (April) and reaches its maximum height by mid-summer
147 (July). The leaves senesce and fall in autumn (October), while the dry leafless stems persist
148 throughout winter (January), unlike *Rubus*, which tends to retain its leaves year-round.

149 Analyses focused exclusively on the herbaceous layer to ensure comparable assessments
150 across vegetation types. Herbaceous species richness was calculated for each plot based on
151 presence-absence botanical data. In spring, herbaceous vegetation cover (%) was visually
152 estimated in three 1m x 1m quadrats installed at random locations in each plot of the
153 vegetation type and across all sites.

154

155 **Plant growth and reproduction traits in spring**

156 Functional traits were measured on the six most abundant herbaceous species identified in the
157 uninvaded riparian forest (control), which are representative of the local herbaceous flora:
158 *Alliaria petiolata* (M.Bieb.)*, Allium ursinum* L., *Ficaria verna* Huds*, Galium aparine* L.*,*
159 *Lamium maculatum* L.*, Veronica hederifolia* L. All six species were found under *Fallopia*,
160 but only three were found under *Rubus*. In each vegetation type, 12 mature and healthy
161 individuals of each species were randomly selected in each plot (reduced to 5 individuals
162 when the species had low abundance).

163 The maximum vegetative length (extended plant length), number of flowers and number of
164 fruits were recorded for all species. Then, individuals of *Ficaria verna*, *Galium aparine* and
165 *Veronica hederifolia* were harvested for destructive trait measurements (root and shoot
166 biomass). Plants were transported to the laboratory and stored at 4°C for a maximum of three
167 days. Aboveground (shoot biomass) and belowground (root biomass) parts were separated,

manually cleaned of soil and rinsed with water. The fresh mass and dry matter content of each organ were determined (±0.0001 g, Denver Instrument) after oven-drying at 65°C for 48h (Memmert).

Statistical analysis

All analyses were performed in R (version 4.5.1, R Core Team, 2025). Each variable was analysed using the lme4 package (Bates et al. 2015). Model selection was performed by backward elimination based on the Akaike information criterion (AIC). All models included sites and plots as random factors. When needed, post-hoc pairwise comparisons were carried out using the emmeans package (Lenth et al. 2018).

Seasonal species richness, and number of flowers and fruits in spring were analysed using generalized linear mixed-effects models (GLMMs) with a binomial distribution and vegetation type as a fixed effect. In addition to vegetation type, season was included as a fixed effect for species richness. Vegetation cover rate, plant length, root and shoot biomass and root biomass allocation (root:shoot ratio) for native species sampled in spring were analyzed using linear mixed-effects models (LMMs) with vegetation type as a fixed effect. For vegetation cover rate, quadrat was included as a random factor. Plant length, root and shoot biomass and root biomass allocation were log-transformed prior to analysis to meet normality assumptions.

For presence-absence data, floristic composition dissimilarities among plots were quantified using Jaccard distances and assessed by permutational multivariate analysis of variance (PERMANOVA, 999 permutations) based on a Euclidean distance matrix in the vegan package (Oksanen et al. 2016). Ordinations were then performed using non-metric

multidimensional scaling (NMDS) to visualize differences among vegetation types across the four seasons studied.

RESULTS

Variations in seasonal species richness

A total of 69 herbaceous species were recorded across the four sites, with few germinations of shrubs or trees (Appendix S1). Season and vegetation type significantly influenced species richness (Season $\chi^2_3 = 8.8$*** | Vegetation type $\chi^2_2 = 10.7$***, Figure 2, Appendix S2). Species richness in winter and summer was lower under *Rubus* than in the control, and intermediate under *Fallopia*. In spring, species richness was higher under *Fallopia* than under *Rubus*, and intermediate in the control. In autumn, species richness was higher in the control than under both *Fallopia* and *Rubus*. Across all three vegetation types, species richness was lower in summer than in spring. For *Fallopia* and *Rubus*, species richness was higher in spring than during the rest of the year.

Dissimilarities in floristic composition

For spring, summer and autumn, pairwise PERMANOVA based on Jaccard dissimilarities revealed significant differences in floristic composition between all vegetation types (Spring $F_2 = 2.64$*** | Summer $F_2 = 2.90$*** | Autumn $F_2 = 3.57$***, Appendix S3). However, no significant difference was detected between *Fallopia* vs control, and *Rubus* vs control in winter, but difference was detected between *Fallopia* and *Rubus* (Winter $F_1 = 2.90$**, Appendix S3).

213 The NMDS ordination highlights this gradual transition between different vegetation types,
214 which begins in spring and results in clearly distinct ellipses by autumn (50% confidence
215 interval, Figure 3). The six species most strongly associated with the ordination axes (envfit,
216 highest R^2 values) are represented as vectors, indicating their contribution to the observed
217 compositional differences. In winter, *Carex pendula* and *Ficaria verna* are associated with
218 *Rubus*, whereas *Galium aparine* and *Poaceae* spp. are associated with *Fallopia*. For every
219 season except winter, *Geum urbanum* and *Hedera helix* are associated with control, and
220 *Galium album* is associated with *Rubus*. In spring and summer, *Solidago virgaurea*,
221 *Saponaria officinalis, Dipsacus sativus* and *Hypericum maculatum* are associated with
222 *Rubus*. In autumn, *Urtica dioica* is associated with *Fallopia*. During its growing season
223 (summer and autumn), *Parthenocissus quinquefolia* was present in all vegetation types within
224 the riparian forest.

225 Perennial species accounted for the largest proportion throughout seasons, mean percentages
226 ranging from 62 to 100 % across all sites and vegetation types (Table 1). Moreover, annuals
227 and biennials disappeared from the uninvaded area during summer and autumn (control at 0
228 %), and remained present in *Fallopia* and *Rubus* throughout the year, with mean percentages
229 ranging from 8 to 16 % during summer and autumn (Table 1).

230

231 **Spring variations in vegetation cover rate**

232 For spring, herbaceous vegetation cover rates revealed significant differences in species
233 abundances between all vegetation types ($\chi^2_2 = 103.8$ ***, Figure 4, Appendix S2).
234 Vegetation cover was significantly higher under *Fallopia* patches than under *Rubus* patches,
235 and comparable to the uninvaded area.

236

237 **Same growth and reproduction under *Fallopia* and control**

238 We selected the six most common herbaceous species found in the uninvaded area, which are
239 representative of the local herbaceous flora. All six were found under *Fallopia*, but only three
240 were found under *Rubus* (*Ficaria verna, Galium aparine* and *Veronica hederifolia*). All
241 statistical results based on functional traits are available in Appendix S4.

242 We first examined the growing traits of herbaceous species. *Galium aparine*, *Veronica*
243 *hederifolia* and *Alliaria petiolata* had a similar length under *Fallopia* compared to the control
244 ($p > 0.05$, Figure 5). *Ficaria verna*, had a similar length under *Fallopia* and under *Rubus* ($p >$
245 0.05, Figure 5). However, *Ficaria verna*, *Allium ursinum* and *Lamium maculatum* had a
246 significantly lower length under *Fallopia* compared to the control ($p < 0.001$***, Figure 5, *F.*
247 *verna* C: 19.9 ± 0.9 cm | F: 15.0 ± 0.7 cm, *A. ursinum* C: 29.3 ± 1.6 cm | F: 23.0 ±1.0 cm, *L.*
248 *maculatum* C: 30.7 ± 1.9 | F: 7.6 ± 0.6 cm). Then, for *Veronica hederifolia*, its length was
249 significantly lower under *Rubus* than under *Fallopia* and in the control ($p < 0.01$**, Figure 5,
250 *V. hederifolia* C: 23.5 ± 1.3 cm, F: 24.4 ± 1.2 cm, R: 21.6 ± 1.3 cm). The three herbaceous
251 growing under *Fallopia* showed the same shoot and root dry mass as those growing in the
252 control. *Galium aparine* under *Fallopia* showed the same shoot and root dry mass as those
253 growing under *Rubus*. However, *Ficaria verna* and *Veronica hederifolia* showed significantly
254 improved shoot dry mass under *Fallopia* compared to those growing under *Rubus* ($p <$
255 0.001***, Figure 5, *F. verna* F: 0.2390 ± 0.0293 g | R: 0.1594 ± 0.0294 g, *V. hederifolia* F:
256 0.0764 ± 0.0086 g | R: 0.0601 ± 0.0104 g). They also showed significantly improved root dry
257 mass under *Fallopia* compared to *Rubus* ($p < 0.05$*, Figure 5, *F. verna* F: 0.0211 ± 0.0021 g |
258 R: 0.0167 ± 0.0026 g and for *V. hederifolia* F: 0.0030 ± 0.0002 g | R: 0.0018 ± 0.0002 g).
259 Then, we did not find any significant differences in root:shoot ratio under the three vegetation
260 types and for the three species ($p > 0.05$, Figure 5).

We next examined the reproductive traits of herbaceous species. We observed that herbaceous flowered and fruited in a similar way in the control and under *Fallopia*, with more flowers for *Lamium maculatum* under *Fallopia* ($p < 0.05$*, Figure 5, *L. maculatum* C: 2 ± 1.3 flowers | F: 7.8 ± 1.9 flowers), and no fruiting in either case. For *Ficaria verna*, the number of flowers under *Rubus* was lower than that observed in the control, and identical to that observed under *Fallopia* ($p < 0.01$**, Figure 5, *F. verna* C: 0.8 ± 0.2 flowers | F: 0.5 ± 0.1 flowers | R: 0.2 ± 0.1 flowers,). For *Alliaria petiolata*, flowering was identical in both conditions ($p > 0.05$, Figure 5).

DISCUSSION

In long-established patches located within the same riparian sites, we investigated how *Fallopia* (invasive non-native) and *Rubus* (invasive native) influence riparian herbaceous communities. By combining species richness, vegetation cover, and functional trait data, we showed that *Fallopia* patches was not associated with lower diversity, abundance or performance than in uninvaded plots (H1), whereas *Rubus* was associated with fewer co-occurring species and lower growth- and reproduction-related traits values (H2). Consistent with our hypotheses, *Fallopia* can promote species coexistence in anthropogenic riparian habitats.

Phenological coexistence

Fallopia patches hosted significantly more species than *Rubus* patches in spring, with a higher vegetation cover rate. In winter, spring and summer, species richness and vegetation cover

283 rates under *Fallopia* were comparable to uninvaded areas. These results contrast with those of
284 Gerber et al. 2008, Hejda et al. 2009 and Aguilera et al. 2010, who found reduced plant
285 diversity in *Fallopia* patches in summer. Studies' differences are likely reflecting seasonal
286 sampling variations, as most surveys were conducted in summer when the overall herbaceous
287 richness declines. Our results highlight the importance of incorporating study context and
288 seasonal dynamics when assessing invasion impacts. The spring coexistence observed under
289 *Fallopia* reveals the availability of a phenological niche for other plant species, which is
290 absent under *Rubus*. Indeed, *Fallopia*'s stems and large leaves emerge as early as April, reach
291 their maximum height in mid-summer, then dry out and fall to the ground in autumn, creating
292 a temporal window of high resource availability (Tokarska-Guzik et al. 2006). This window
293 allows native herbaceous species with contrasting phenologies to complete key life stages
294 before *Fallopia*'s canopy closes, unliked the more consistently closed canopy of *Rubus*
295 (Keller and Shea 2021, Cleland and Wolkovich 2024). During summer, dense *Fallopia* stands
296 reduce light availability near the ground, but similar shading could occur under the uninvaded
297 area due to riparian canopy development. In this sense, *Fallopia* stands could support species
298 adapted to seasonal light fluctuations (Goodenough 2010, Matysiak 2021). If certain species
299 perform better under *Fallopia* than under *Rubus* and comparably under uninvaded area in
300 spring, this suggests that an ecological niche may be shared or even created within *Fallopia*
301 patches (Odling-Smee et al. 1996).

302

303 Life-history strategies further modulate this species coexistence. Perennials dominated across
304 all conditions, whereas annuals were largely absent in summer and autumn in uninvaded
305 areas. Annual species, adapted to temporally variable environments, can exploit brief high-
306 light periods in early spring to complete their life cycle before shading intensifies (Friedman

2020, Cleland and Wolkovich 2024). Thus, seasonal resource dynamics under both *Fallopia* and *Rubus* selectively filter species according to phenology.

Evidence for no competition

In spring, several herbaceous species were absent from *Rubus* patches, and *Veronica hederifolia* exhibited reduced growth and reproductive traits under *Rubus*. These results are consistent with previous work showing competitive effects and litter inhibition of root development for *Rubus* (Staentzel et al. 2020). By contrast, *Alliaria petiolata* and *Veronica hederifolia* completed their life cycle until fruits production within *Fallopia* patches and in uninvaded areas, with both exhibiting the same plant length. Some species such as *Lamium maculatum*, even showed enhanced reproductive traits under *Fallopia* than in the uninvaded area, with a higher number of flowers. This aligns with previous studies reporting successful germination, growth, and flowering of native species (*Ficaria verna*, *Allium ursinum*, *Hyacinthoides non-scipta*, *Veronica hederifolia* and *Galium aparine*) within *Fallopia* patches (Tokarska-Guzik et al. 2006, Goodenough 2010, Maurel et al. 2010, Matysiak 2021, Lee et al. 2024). Together, these findings support the existence of a favorable period that enables early-season species to prosper in the same environment despite competition for similar resources (Holt 2001).

Functional trait responses further suggest that native species maintain substantial growth potential under *Fallopia*, with no differences in biomass relative to uninvaded areas. In its native range, *Fallopia* acts as a pioneer species that enriches soils with nitrogen and thereby enabling coexistence of higher nitrogen-demands herbaceous (Tateno and Hirose 1987, Dassonville et al. 2007). Its ability to alter nitrogen cycling through denitrification inhibition (BDI) may enhance nutrient availability (Bardon et al. 2014), allowing the establishment of

331 species such as *Urtica dioica*. More broadly, positive interactions between native and non-
332 native species may promote species coexistence through resource partitioning and niche
333 differentiation (Bartomeus and Godoy 2018, Cantarel et al. 2020). By modifying abiotic
334 conditions and introducing novel physical structure, *Fallopia* can create opportunities for
335 nutrient enrichment to hosted plants (Rodriguez 2006). Plants coexistence may be for example
336 possible through spatial niche differentiation with variation in rooting depth (MacDougall et
337 al. 2009, Adler et al. 2013). These results suggest that positive interactions involving non-
338 native species may be more widespread than often assumed and could demonstrate the
339 existence of resource sharing among species coexisting in patches. One-year experimental
340 monitoring of soil nitrogen levels at study sites would help support these hypotheses.

341

342 **Functional roles in modified ecosystems**

343 Floristic composition varied seasonally across vegetation types, indicating that *Fallopia*,
344 *Rubus* and uninvaded areas each contribute to habitat heterogeneity. Differences in species
345 composition reflect contrasting ecological preferences, with some species preferentially
346 associated with invaded or uninvaded conditions. Of the 69 herbaceous plants identified, only
347 two were invasive non-native species (*Parthenocissus quinquefolia* and *Solidago gigantea)*,
348 which means that *Fallopia* and *Rubus* may host native biodiversity in this riparian ecosystem.
349 The low occurrence of woody species likely reflects the position of these communities along a
350 disturbance gradient. In the studied alluvial system, stages of succession ranging from shrubs
351 to trees can be observed, with *Fallopia* and *Rubus* located in the shrub part (Bottollier-Curtet
352 et al. 2011). This part is exposed to frequent hydrological disturbances that play an important
353 role in the dynamics of riparian vegetation establishment (Bendix and Hupp 2000, Boedeltje
354 et al. 2004). However, the hydrological regime of the Ain river studied here is subject to rapid

and significant fluctuations in flow caused by hydroelectric dams regulation (Alp et al. 2023, Judes et al. 2023) and limits plants establishment by reducing seedling survival (Bejarano et al. 2018, 2020). For certain species, *Fallopia* may allow substrate stabilization, propagules trapping, and hydrological stress buffering (Bendix and Hupp 2000, Bruno et al. 2003, Badano et al. 2016). Such effects can enhance local heterogeneity and facilitate the establishment of riparian native herbaceous (Rodriguez 2006, Schlaepfer et al. 2011, Vega-Álvarez et al. 2019).

These findings support the view that non-native habitat formers may provide valuable functions (Ramus et al. 2017). While invasive species are often associated with biodiversity loss, they may also provide functional substitutes in highly altered environments (Hobbs et al. 2009, Carroll 2011, Truitt et al. 2015, De Bello et al. 2021).

Toward a more nuanced approach to plant invasions

Our results challenge the strictly negative perception of non-native invasives and calls for a more nuanced approach. Not all introduced species constitute a threat to biodiversity, nor do they systematically alter the composition of local species (Rémy and Beck 2008). In this studied hydrosystem, *Fallopia* supported a relatively diverse herbaceous community, including species absent from *Rubus* patches. Notably, *Rubus* is not typically targeted for management and research despite its competitive effects, as persistent patches can resist re-invasion by trees (Widen et al. 2018, Cottet et al. 2018, 2020). These selective foci, often linked to partisan choices in response variables or unbalanced study designs, may favor certain hypotheses over others and risks obscuring the complexity of ecological interactions (Hulme et al. 2013, Warren et al. 2017, Guiaşu and Tindale 2018, Losapio 2023).

These findings call for a more context-dependent and evidence-based approach to invasion management (Schlaepfer et al. 2011, Hulme et al. 2013, Thomsen and Wernberg 2015). Alarmist generalizations may overlook cases where non-native species provide ecological functions. The 'guilty until proven innocent' approach applied to *Fallopia* is detrimental as it can lead to control programs targeting species that are harmless or even beneficial (Sagoff 2018, Guiaşu and Tindale 2018). In the studied hydrosystem, factors such as flow regulation, land-use change, and habitat fragmentation likely play a primary role in biodiversity decline (Schnitzler and Muller 1998, Tokarska-Guzik et al. 2006, Motta 2025). Within this context, *Fallopia* may contribute to maintaining seasonal diversity and ecosystem functioning at levels comparable to those observed in uninvaded area. However, assessing the positive effects of non-native species should not be seen as an attempt to ignore the negative ones, but rather as an opportunity to refines management priorities (Tassin et al. 2017, Vimercati et al. 2020). For instance, if *Fallopia* patches host persistent seed banks of native species, intensive disturbance-based control methods could inadvertently reduce native biodiversity (Lee et al. 2024). Identify non-natives species as a potential host for biodiversity into decision-making processes may therefore improve conservation outcomes (D'Antonio and Meyerson 2002, Ramus et al. 2017).

Incorporating the functional roles of non-native species into management and research frameworks may help design more resilient ecosystems under ongoing environmental changes (D'Antonio and Meyerson 2002, Ramus et al. 2017, Kharouba 2024). A potential internal reorganization of vegetal communities is inevitable, especially if non-native species with similar functional roles can replace those that have been lost (Oliver et al. 2015, Chaffin et al. 2016, Kharouba 2024). At the same time, attention should remain focused on the underlying drivers of degradation, including climate change and human land use, which primarily shape ecosystems dynamics.

CONCLUSIONS

Our observational field study shows that long-established *Fallopia* supports plant species diversity at levels comparable to uninvaded areas, and to a greater extent than *Rubus*. This pattern of long-term co-occurrence may be related to the creation of an available temporal phenological niche, via seasonal differences in canopy development and resource availability within *Fallopia* patches. Differences in traits related to plant growth and reproduction among co-occurring herbaceous species may reflect variation in environmental filtering, phenological overlap, or competitive conditions. Distinguishing among these explanations, and assessing their consequences for demographic performance, resource partitioning, and stable coexistence, will require multi-year demographic measurements. Our results nevertheless show that the associations and potential ecological functions of non-native plants and riparian herbaceous communities in human-altered systems may be context dependent and cannot be predicted from biogeographic origin alone.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All data and code with this research (de La Forge et al., 2026) are available from data.gouv.fr.

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AUTHORS' CONTRIBUTIONS

Irène de La Forge, Amélie A. M. Cantarel, Marylise Cottet and Florence Piola: conceptualization - Irène de La Forge, Amélie A. M. Cantarel, Christelle Boisselet, Emma Silvestre and Florence Piola: methodology - Irène de La Forge, Christelle Boisselet, Florence Piola and Emma Silvestre: data collection - Irène de La Forge and Emma Silvestre: data analysis, Irène de La Forge, Amélie A. M. Cantarel, Marylise Cottet and Florence Piola: supervision. All authors contributed to the drafts and gave final approval for publication.

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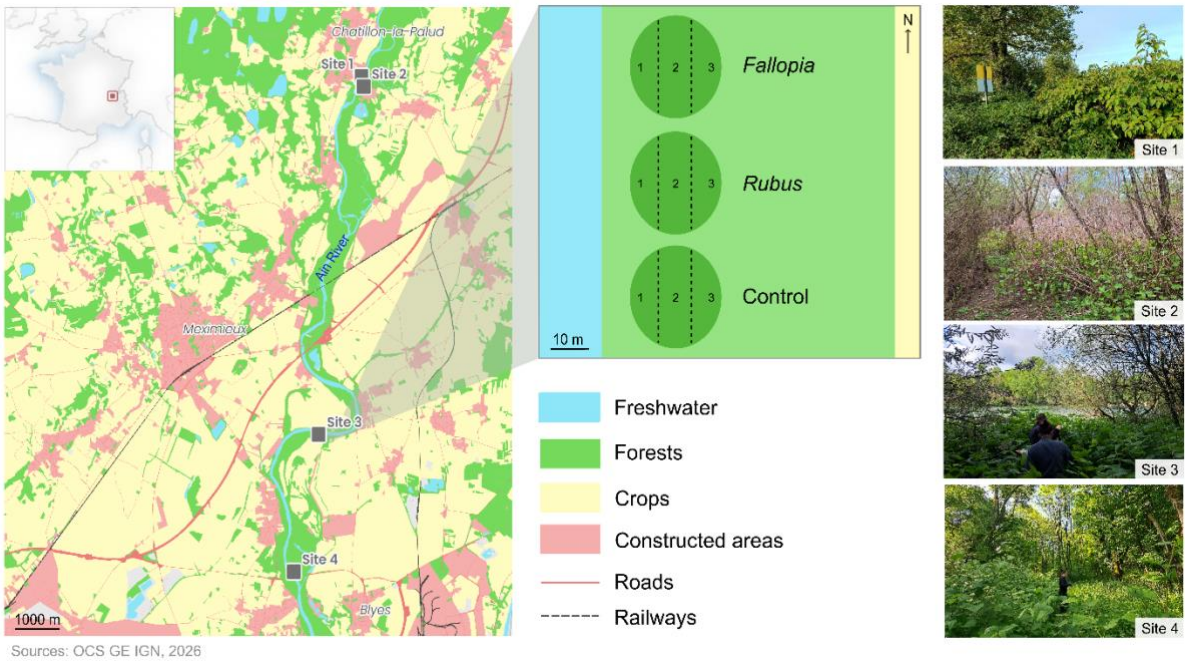
667 168.
668
669

TABLE

TABLE 1

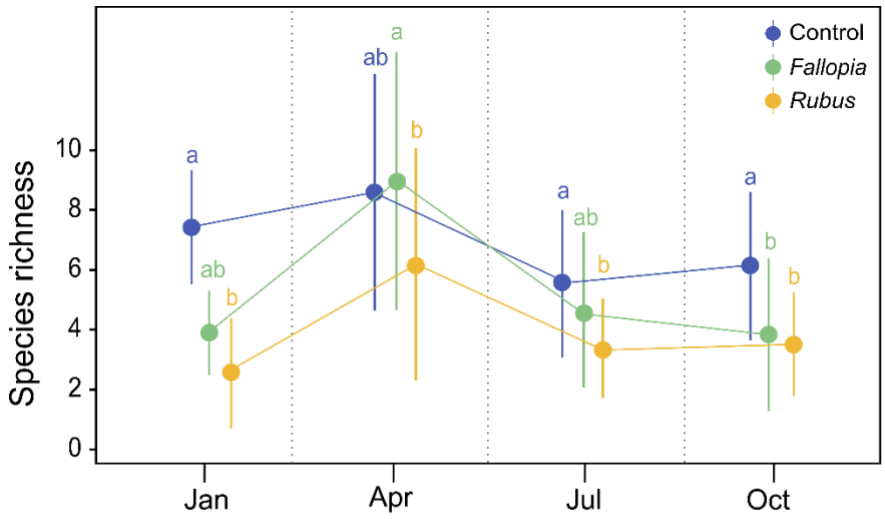
Season	Vegetation type	Life cycle		
		Annual (%)	**Biennial (%)**	**Perennial (%)**
Winter	Control	25 ± 11	13 ± 3	62 ± 13
	Fallopia	21 ± 13	14 ± 2	68 ± 6
	Rubus	44 ± 39	18 ± 2	62 ± 20
Spring	Control	16 ± 3	6 ± 2	83 ± 12
	Fallopia	18 ± 12	14 ± 4	71 ± 7
	Rubus	25 ± 18	14 ± 6	68 ± 19
Summer	Control	0	7 ± na	98 ± 4
	Fallopia	15 ± na	15 ± na	92 ± 15
	Rubus	9 ± na	16 ± 9	90 ± 12
Autumn	Control	0	0	100
	Fallopia	8 ± na	11 ± na	95 ± 6
	Rubus	11 ± 2	13 ± 5	88 ± 8

FIGURES



677

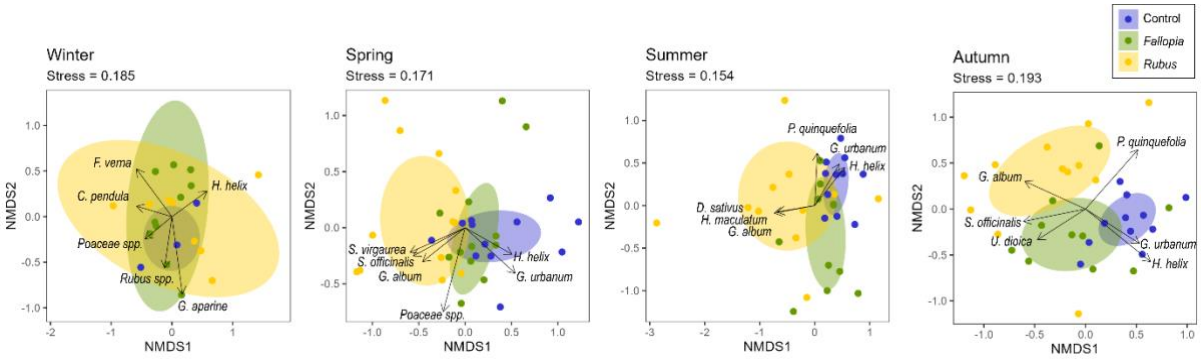
678 **FIGURE 1**



	Winter	Spring	Summer	Autumn
Control	8.00 ± 1.15 AB	9.17 ± 1.25 A	6.08 ± 0.72 B	6.70 ± 0.73 AB
Fallopia	4.40 ± 0.45 B	9.58 ± 1.31 A	5.08 ± 0.80 B	4.25 ± 0.78 B
Rubus	3.00 ± 0.61 A	6.67 ± 1.19 A	3.75 ± 0.51 B	3.92 ± 0.51 B

679

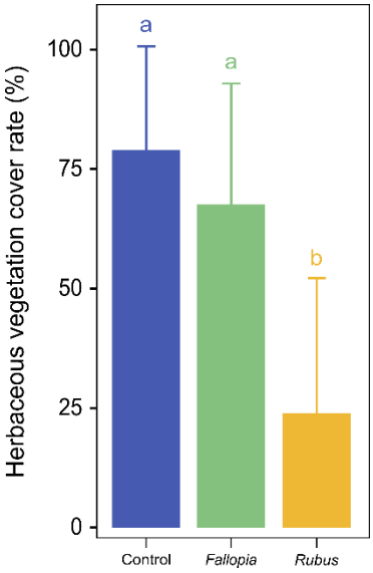
680 **FIGURE 2**



681

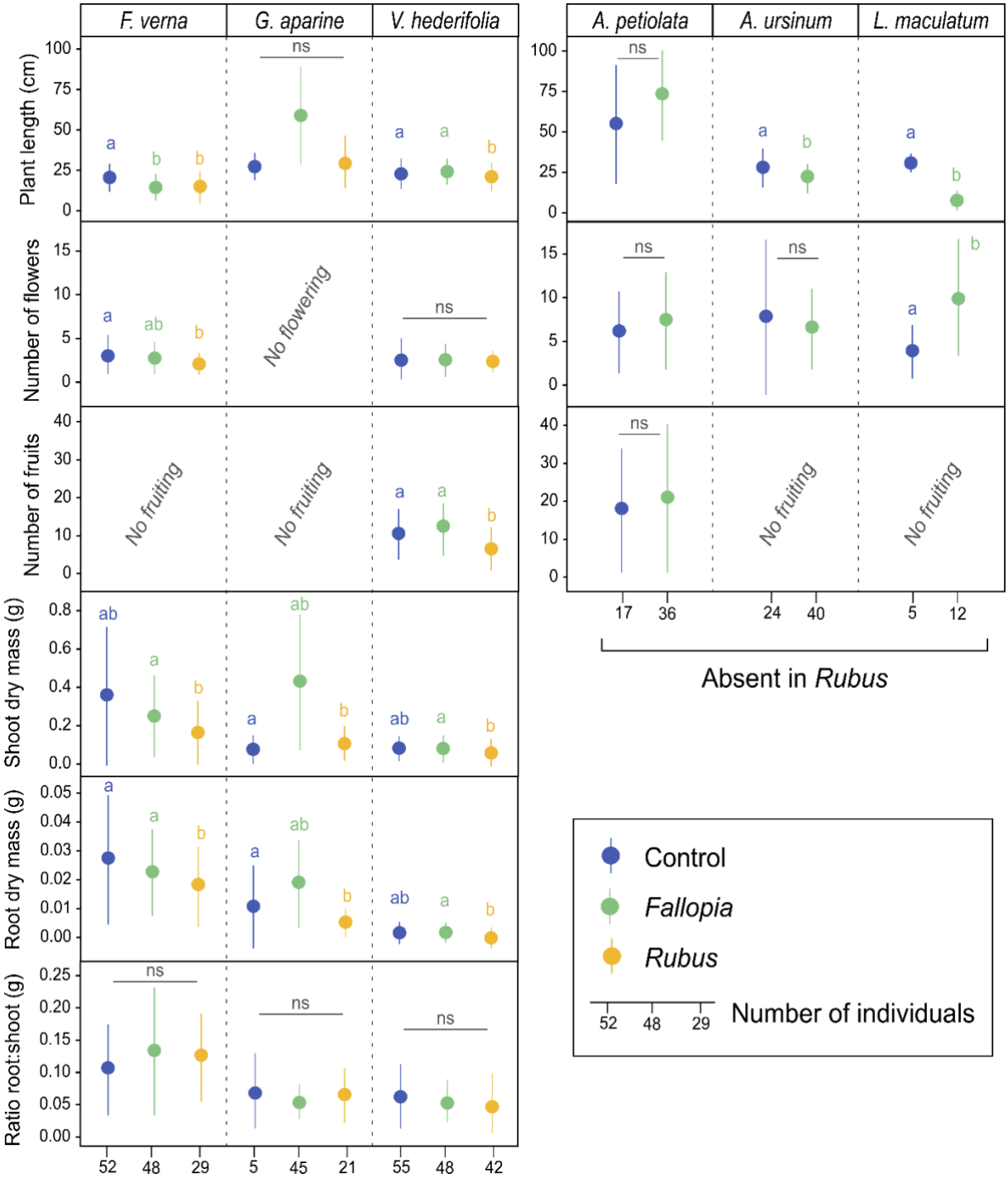
682 **FIGURE 3**

683



684

685 **FIGURE 4**



686

687 **FIGURE 5**

688

689

TABLE LEGEND

TABLE 1. Percentage of annuals, biennials and perennials herbaceous species recorded under the three different vegetation types for each season. Values (mean ± SD) were compared between non-native (*Fallopia*), native (*Rubus*) and uninvaded area (control), with mean ± na indicating insufficient sample size.

FIGURE LEGENDS

FIGURE 1. The Ain River region and the sampling design. The river is located in eastern France. The four sites are part of a hydrosystem under anthropogenic influence. The three vegetation types sampled in the riparian forest were the non-native (*Fallopia*), the native species (*Rubus*) and an uninvaded area (control). Each area included three equal plots (3 x 3 m).

FIGURE 2. Herbaceous species richness recorded under the three different vegetation types for each season. Values (mean ± SD) were compared between non-native (*Fallopia*), native (*Rubus*) and uninvaded area (control). Different minuscule letters indicate significant differences among season, and different capital letters indicate significant differences among vegetation type (generalized linear mixed-effect model with *post-hoc* Emmeans tests, $p < 0.001$***).

FIGURE 3. Floristic composition in the three different vegetation types illustrated by Nonmetric Multidimensional Scaling (NMDS). Differences in species composition are represented according to Jaccard dissimilarities (presence-absence) with an acceptable stress level of less than 0.2. The six most explanatory species are illustrated by arrows (*Carex pendula, Dipsacus sativus, Ficaria verna, Galium album, Galium aparine, Geum urbanum,*

713 *Hedera helix, Hypericum maculatum, Parthenocissus quinquefolia, Saponaria officinalis,*
714 *Solidago virgaurea, Urtica dioica*). 50% confidence interval ellipses are displayed for each
715 vegetation type. For control in winter with insufficient sample size (n=3), the ellipse is drawn
716 based on group centroid and dispersion for greater clarity.

717 **FIGURE 4.** Herbaceous vegetation cover rates recorded under the three different vegetation
718 types in spring. Values (mean ± SD) were compared between non-native (*Fallopia*), native
719 (*Rubus*) and uninvaded area (control). Different letters indicate significant differences among
720 vegetation types (linear mixed-effect models with *post-hoc* Emmeans tests, $p < 0.001$***).

721 **FIGURE 5.** Comparisons of growth and reproduction traits for each native species sampled
722 in the three different vegetation types. Values (mean ± SD) for n individuals (*Ficaria verna,*
723 *Galium aparine, Veronica hederifolia, Alliaria petiolata, Allium ursinum, Lamium*
724 *maculatum*) were compared between non-native (*Fallopia*), native (*Rubus*) and uninvaded
725 area (control). Different letters indicate significant differences among species (generalized
726 linear mixed-effect models for number of flowers and number of fruits; linear mixed-effect
727 models for length, shoot, root and root:shoot ratio dry mass | with *post-hoc* Emmeans tests, p
728 < 0.05*).

729 **Supplementary data**

730 **Appendix S1. Description and sampling details of the 69 herbaceous species used in the**
731 **study.** *Fallopia* x *bohemica* and *Rubus caesius* could be found as isolated individuals within
732 the patches. Except for *Fallopia* spp., only two species are considered invasive alien species in
733 Europe (*Parthenocissus quinquefolia* and *Solidago gigantea*). Colors indicate species identified
734 in the different vegetation types C: Control (blue), F: *Fallopia* spp. (green), R: *Rubus* spp.
735 (yellow).

Species names	Family	Life cycle	Observation season	C	F	R
Aegopodium podagraria	Apiaceae	Perennial	Winter, Spring, Summer, Autumn			
Aethusa cynapium	Apiaceae	Annual	Spring			
Agrimonia eupatoria	Rosaceae	Perennial	Summer, Autumn			
Alliaria petiolata	Brassicaceae	Bisannual	Winter, Spring, Summer			
Allium ursinum	Amaryllidaceae	Perennial	Winter, Spring			
Anemone ranunculoides	Ranunculaceae	Perennial	Spring			
Anthriscus caucalis	Apiaceae	Annual	Spring			
Arctium nemorosum	Asteraceae	Bisannual	Spring			
Artemisia vulgaris	Asteraceae	Perennial	Spring, Summer			
Arum maculatum	Araceae	Perennial	Winter, Spring, Summer			
Barbarea vulgaris	Brassicaceae	Bisannual	Spring			
Boehmeria cylindrica	Urticaceae	Perennial	Spring			
Cardamine hirsuta	Brassicaceae	Annual	Winter, Spring			
Cardamine pratensis	Brassicaceae	Perennial	Spring, Summer, Autumn			
Carex pendula	Cyperaceae	Perennial	Winter, Spring, Summer, Autumn			
Circaea alpina	Onagraceae	Perennial	Spring, Summer, Autumn			
Convolvulus arvensis	Convolvulaceae	Perennial	Spring, Summer, Autumn			
Dipsacus sativus	Caprifoliaceae	Bisannual	Spring, Summer, Autumn			
Fallopia x bohemica	Polygonaceae	Perennial	Summer, Autumn			
Ficaria verna	Ranunculaceae	Perennial	Winter, Spring			
Fragaria viridis	Rosaceae	Perennial	Summer, Autumn			
Galium album	Rubiaceae	Perennial	Spring, Summer, Autumn			
Galium aparine	Rubiaceae	Annual	Winter, Spring, Autumn			
Galeopsis tetrahit	Lamiaceae	Annual	Summer			
Geranium molle	Geraniaceae	Annual	Spring			
Geranium robertianum	Geraniaceae	Perennial	Spring, Summer, Autumn			
Geum urbanum	Rosaceae	Perennial	Winter, Spring, Summer, Autumn			
Geum sylvaticum	Rosaceae	Perennial	Autumn			
Glechoma hederacea	Lamiaceae	Perennial	Spring, Summer, Autumn			
Glechoma hirsuta	Lamiaceae	Perennial	Spring			
Hedera helix	Araliaceae	Perennial	Winter, Spring, Summer, Autumn			
Heracleum sphondylium	Apiaceae	Bisannual	Spring			
Hesperis matronalis	Brassicaceae	Bisannual	Summer, Autumn			
Hypericum maculatum	Hypericaceae	Perennial	Spring, Summer, Autumn			

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Species names	Family	Life cycle	Observation season	C	F	R
Lamium galeobdolon	Lamiaceae	Perennial	Spring, Summer			
Lamium maculatum	Lamiaceae	Perennial	Spring, Summer, Autumn			
Lamium purpureum	Lamiaceae	Annual	Winter, Spring, Summer			
Lysimachia nummularia	Primulaceae	Perennial	Summer			
Lythrum salicaria	Lythraceae	Perennial	Summer			
Mentha arvensis	Lamiaceae	Perennial	Spring			
Narcissus pseudonarcissus	Amaryllidaceae	Perennial	Spring			
Origanum vulgare	Lamiaceae	Perennial	Summer, Autumn			
Parietaria officinalis	Urticaceae	Perennial	Spring, Summer, Autumn			
Parthenocissus quinquefolia	Vitaceae	Annual	Spring, Summer, Autumn			
Persicaria hydropiper	Polygonaceae	Perennial	Summer, Autumn			
Plantago lanceolata	Plantaginaceae	Perennial	Spring			
Poaceae spp.	Poaceae	Perennial	Winter, Spring, Summer, Autumn			
Potentilla reptans	Rosaceae	Perennial	Autumn			
Ribes rubrum	Grossulariaceae	Perennial	Spring			
Rosa canina	Rosaceae	Perennial	Spring			
Rubus caesius	Rosaceae	Perennial	Winter, Spring, Summer, Autumn			
Rumex conglomeratus	Polygonaceae	Perennial	Spring			
Rumex crispus	Polygonaceae	Bisannual	Spring			
Rumex pulcher	Polygonaceae	Perennial	Spring			
Rumex spp.	Polygonaceae	Perennial	Summer, Autumn			
Saponaria officinalis	Caryophyllaceae	Perennial	Spring, Summer, Autumn			
Scrophularia nodosa	Scrophulariaceae	Perennial	Spring			
Senecio ovatus	Asteraceae	Annual	Spring			
Silene noctiflora	Caryophyllaceae	Perennial	Spring			
Solidago gigantea	Asteraceae	Perennial	Summer, Autumn			
Solidago virgaurea	Asteraceae	Perennial	Winter, Spring			
Stellaria aquatica	Caryophyllaceae	Perennial	Summer			
Symphyotrichum lanceolatum	Asteraceae	Perennial	Autumn			
Taraxacum officinale	Asteraceae	Perennial	Spring, Summer, Autumn			
Urtica dioica	Urticaceae	Bisannual	Winter, Spring, Summer, Autumn			
Verbascum phlomoides	Scrophulariaceae	Bisannual	Spring			
Verbena officinalis	Verbenaceae	Annual	Summer, Autumn			
Veronica hederifolia	Plantaginaceae	Perennial	Winter, Spring, Autumn			
Veronica montana	Plantaginaceae	Perennial	Spring, Summer, Autumn			
Veronica serpyllifolia	Plantaginaceae	Perennial	Spring			

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Appendix S2. Results from generalized linear mixed-effects models (GLMMs) on seasonal species richness and linear mixed-effects models (LMMs) on vegetation cover rate in spring. Both models included vegetation type as a fixed effect, site and position as a random factor. For seasonal species richness, season was included as a fixed effect. For vegetation cover rate in spring, quadrat was included as a random factor. Variables marked with "-" indicate those that were not used. Significance levels are: p<0.05*; p<0.01**; p<0.001***.

	X^2	df	*p*- value	X^2	df	*p*- value
	Seasonal species richness			**Vegetation cover rate in spring**		
All	95.7	1	<<0.001 ***	198.9	1	<<0.001 ***
Vegetation type	10.7	2	<0.001 ***	103.8	2	<<0.001 ***
Season	8.8	3	<0.001 ***	-	-	-

Appendix S3. Results from permutational multivariate analysis of variance (PERMANOVA, 999 permutations, function *adonis* in R) based on Jaccard dissimilarities (presence/absence species matrix). Significance levels are: p<0.05*; p<0.01**; p<0.001***.

	Winter				Spring				Summer				Autumn			
	Df	R2	F	p value	Df	R2	F	p value	Df	R2	F	p value	Df	R2	F	p value
All	2	0.19	2.39	0.003 **	2	0.13	2.64	0.001 ***	2	0.15	2.90	0.001 ***	2	0.19	3.57	0.001 ***
Fallopia spp. vs Control	1	0.13	1.87	0.097	1	0.09	2.24	0.003 **	1	0.11	2.52	0.021 *	1	0.12	2.82	0.007 **
Fallopia spp. vs *Rubus* spp.	1	0.13	2.90	0.007 **	1	0.10	2.55	0.002 **	1	0.10	2.37	0.01 **	1	0.10	2.21	0.01 **
Rubus spp. vs Control	1	0.17	2.08	0.057	1	0.12	3.10	0.001 ***	1	0.15	3.78	0.001 ***	1	0.20	5.66	0.001 ***

Appendix S4. Results from generalized linear mixed-effects models (GLMMs) on number of flowers and fruits, and results from linear mixed-effects models (LMMs) on length, shoot, root and ratio root:shoot dry mass. All models included vegetation type as a fixed effect and site as a random factor. Shoot, root and ratio root:shoot dry mass were log-transformed prior to analyses. Variables marked with "-" indicate those that were not used. Significance levels are: p<0.05*; p<0.01**; p<0.001***.

		Ficaria verna			*Galium aparine*			*Veronica hederifolia*			*Alliaria petiolata*			*Allium ursinum*			*Lamium maculatum*		
		X^2	df	*p*-value	X^2	df	*p*-value	X^2	df	*p*-value	X^2	df	*p*-value	X^2	df	*p*-value	X^2	df	*p*-value
Plant lenght																			
	All	385.9	1	<<0.001 ***	13.2	1	<0.001 ***	65.3	1	<<0.001 ***	5.5	1	0.01*	250.9	1	<<0.001 ***	93.3	1	<<0.001 ***
	Vegetation type	19.1	2	<0.001 ***	1.1	2	0.56	9.2	2	<0.01 **	7.3	1	<0.01 **	14.0	1	<0.001 ***	27.8	1	<<0.001 ***
Number of flowers																			
	All	1.1	1	0.28	-	-	-	3.9	1	0.04 *	0.4	1	0.51	2.3	1	0.12	1.6	1	0.20
	Vegetation type	10.9	2	<0.01 **	-	-	-	2.6	2	0.27	0.1	1	0.97	2.0	1	0.15	4.6	1	<0.05 *
Number of fruits																			
	All	-	-	-	-	-	-	298.0	1	<<0.001 ***	0.5	1	0.47	-	-	-	-	-	-
	Vegetation type	-	-	-	-	-	-	77.5	2	<<0.001 ***	2.9	1	0.08	-	-	-	-	-	-
Shoot dry mass																			
	All	100.9	1	<<0.001 ***	29.6	1	<<0.001 ***	112.7	1	<<0.001 ***	-	-	-	-	-	-	-	-	-
	Vegetation type	12.3	2	<0.001 ***	27.8	2	<<0.001 ***	14.0	2	<0.001 ***	-	-	-	-	-	-	-	-	-
Root dry mass																			
	All	656.6	1	<<0.001 ***	100.4	1	<<0.001 ***	1617.1	1	<<0.001 ***	-	-	-	-	-	-	-	-	-
	Vegetation type	7.3	2	<0.05 *	37.0	2	<<0.001 ***	43.2	2	<<0.001 ***	-	-	-	-	-	-	-	-	-
Root:Shoot dry mass																			
	All	338.4	1	<<0.001 ***	95.5	1	<<0.001 ***	256.1	1	<<0.001 ***	-	-	-	-	-	-	-	-	-
	Vegetation type	3.4	2	0.18	0.2	2	0.99	2.4	2	0.30	-	-	-	-	-	-	-	-	-