

**PREPRINT**

*Author-formatted, not peer-reviewed document posted on 28/06/2024*

DOI: <https://doi.org/10.3897/arphapreprints.e130649>

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**Biotic interactions more than abiotic conditions  
determine the invasion success of *Senecio inaequidens*  
DC.**

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3 **Biotic interactions more than abiotic conditions determine the invasion success of**  
4 ***Senecio inaequidens* DC.**

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13

14 **Abstract**

15 Invasive alien species pose significant threats to global biodiversity and ecosystems.  
16 Given the high importance of context-dependency in invasion dynamics, testing  
17 fundamental hypotheses of invasion ecology in different environmental contexts is crucial  
18 to understand the underlying processes of the establishment and spread of alien species.  
19 This study focuses on the invasive alien *Senecio inaequidens* DC. (South African ragwort),  
20 investigating the interplay between abiotic and biotic factors influencing its invasion  
21 success. Through field surveys across three semi-natural habitats in Northern Italy, we  
22 assessed the relative importance of abiotic (soil characteristics) and biotic (resident  
23 vegetation diversity and similarity to the target alien) variables on *S. inaequidens*  
24 performance. Our results showed a pivotal role of biotic interactions over abiotic conditions  
25 in determining the success of the alien species. We found evidence of biotic resistance by  
26 resident plant communities, and it was mainly explained by resident species' diversity and  
27 cover. However, when analysing the similarity patterns between *S. inaequidens* and the  
28 invaded communities, we surprisingly found a negative relationship between *S.*  
29 *inaequidens* success and similarity to resident communities, indicating a better  
30 performance of the alien species when growing with more similar species. Abiotic factors  
31 had only marginal effects on influencing the strength and direction of biotic interactions

32 and partially showed a stronger biotic resistance (in terms of resident species richness) in  
33 more benign abiotic conditions (soil with higher nutrient concentrations and in habitats less  
34 disturbed and stressed). Therefore, *S. inaequidens* appears to be more susceptible to  
35 competition rather than adverse abiotic conditions, making it a good colonizing species  
36 rather than a strong competitor, which might imply that in ruderal or stressed environments  
37 being functionally similar to the recipient communities could confer this species an  
38 advantage to invade. Our findings underscore the complexity of invasion dynamics,  
39 highlighting the need to consider diverse mechanisms, including taxonomic, phylogenetic,  
40 and functional measures, as well as the abiotic context, to inform effective management  
41 strategies for invaded ecosystems.

42

### 43 **Keywords**

44 Biotic resistance, environmental filtering, *Senecio inaequidens*, diversity-invasibility, pre-  
45 adaptation.

46

### 47 **Introduction**

48 Invasion by alien species is considered one of the main drivers of biodiversity loss  
49 worldwide, with well documented economic and human health-related impacts (IPBES  
50 2023). As the number of introduced alien taxa continues to rise steadily (Seebens et al.  
51 2021), it is expected that this will pose significantly higher economic costs for their  
52 management and control, as well as ecological impacts (Hejda et al. 2009, Vilà et al. 2011,  
53 Schindler et al. 2015, Gentili et al. 2019, Henry et al. 2023). Therefore, understanding the  
54 underlying processes leading to the successful invasion of alien plants is crucial for  
55 predicting their potential spread and impacts (Carboni et al. 2018) and to efficiently plan  
56 habitat restoration and environmental management practices in invaded communities (El-  
57 Barougy et al., 2020).

58 Invasion is usually conceptualized as a staged process, where each stage is divided by a  
59 filter to be overcome by the invader. The exact number and definition of such stages can  
60 be variable in the literature, but generally all stages begin with transport and introduction of  
61 plant/plant-propagules and culminate with species' spread and potentially negative impacts  
62 (Richardson et al. 2000; Catford et al. 2009; Blackburn et al. 2011). Using a synthesis on  
63 29 leading hypotheses in invasion ecology, Catford et al. (2009) postulated that there are

64 three main ecological processes that play a role determining the invasion success within  
65 native communities: (i) introduction, (ii) environmental filtering, and (iii) biotic interactions  
66 between the alien and resident species. The combination of these three processes  
67 determines whether a community will be invaded or not.

68 Introduction first depends on propagule pressure (i.e., the number of individuals introduced  
69 in an event multiplied by the frequency of the introduction events (Eppstein & Molofsky  
70 2007)), with the expectation that higher propagule pressures may promote invasions by  
71 enhancing genetic diversity of the already introduced populations and by increasing the  
72 probability of introduction in more favourable environments (Lockwood et al. 2005, Catford  
73 et al. 2009). However, once introduced into a new area, the environmental characteristics  
74 must be suitable for the alien plant, since abiotic conditions related to, e.g., temperature,  
75 nutrient, and water availability can represent a filter for species not adapted to the new  
76 conditions (Carboni et al. 2018). If the abiotic filters have been successfully overcome and  
77 the alien plant is able to survive and reproduce under the new conditions, invasion  
78 success will also depend on interactions with species in the recipient communities  
79 (Carboni et al. 2018). For instance, competitive interactions can result in the biotic  
80 resistance of the recipient communities (Elton 1958; Levine et al. 2004; Daly et al. 2023),  
81 limiting the successful establishment and/or spread of invading alien plants (Byun et al.  
82 2015).

83 Biotic resistance, a hypothesis rooted in competition theory (Case 1990), can be defined  
84 as the ability of native communities to hinder invasion by alien plants (Levine et al. 2004).  
85 The underlying assumption being that in resource limited environments, alien plants can  
86 only successfully invade communities lacking species occupying similar niches because  
87 niche overlap will lead to intense competition (MacDougall et al. 2009). For instance,  
88 highly diverse ecosystems can be more resistant to invasion due to higher chances of the  
89 recipient community of covering a broader spectrum of niches (known as diversity-  
90 invasibility hypothesis (Elton 1958; Jeschke 2014)), leading to a negative correlation  
91 between native species diversity and alien species presence (measured as richness,  
92 functional and/or phylogenetic diversity; see e.g., Feng et al. (2019)). In addition, similarity  
93 patterns between alien and recipient communities, measured using functional traits or  
94 phylogenetic distances, have also been explored to explain biotic resistance (Yannelli et al.  
95 2017). Specifically, alien species have been proposed to successfully invade functionally  
96 dissimilar communities (MacArthur and Levins 1967) measured either by functional traits  
97 (limiting-similarity hypothesis (Funk et al. 2008; Yannelli et al. 2017)), or by phylogenetic

98 distances (Darwin's naturalization hypothesis (Darwin 1859; Daehler 2001; Yannelli et al.  
99 2017; Sheppard et al. 2018)). From a phylogenetic perspective, the assumption is that  
100 species relatedness can be used as a proxy for similarity of traits, provided that they are  
101 conserved in the phylogeny (Cahill et al. 2008). However, evidence supporting these  
102 hypotheses is mixed, indicating that different patterns in the field can emerge, depending  
103 on the spatial scale, the stage of the invasion process considered and even the metrics  
104 used (Levine and D'Antonio 1999; Cleland et al. 2004; Smith and Côté 2019; Ernst et al.  
105 2022).

106 Moreover, it must be emphasised that both environmental filtering and biotic interactions  
107 act at the same time in a dynamic way to shape species assembly patterns. For instance,  
108 alien plants can be facilitated by changes of abiotic conditions that adversely affect  
109 natives, or can be inhibited by specific abiotic characteristics, ultimately enhancing biotic  
110 resistance (Byun et al. 2015). Indeed, numerous studies have highlighted how variations in  
111 abiotic characteristics can strongly influence the nature and intensity of biotic interactions  
112 in a community (see e.g., Von Holle, 2005; Kraft et al., 2015; Byun et al. 2022).  
113 Competition is expected to play a more significant role in benign conditions, where native  
114 communities are likely to be more productive. Conversely, in harsher and more stressful  
115 environments (intense abiotic filtering), or in disturbed contexts, the effects of competitive  
116 interactions could be reduced (Grime 1973, Brose and Tielbörger 2005, Gallien and  
117 Carboni 2017). Understanding the interplay of abiotic filters and biotic interactions among  
118 species in the recipient community and those introduced is crucial for elucidating the  
119 factors shaping patterns of plant invasions observed in the field (Zarnetske et al. 2013).

120 From these premises, it emerges that the context in which invasions take place matters, as  
121 it can determine whether, when, and where alien species succeed or fail to become  
122 invasive, as well as which systems are resistant or prone to be invaded (Catford et al.  
123 2022). Therefore, it is particularly important to understand the context dependency of the  
124 invasion process to predict future invasions as well as implement effective management  
125 strategies (Catford et al. 2022). Testing fundamental hypotheses of invasion ecology in  
126 different habitats and environmental conditions becomes therefore a key aspect to fully  
127 understand the underlying mechanisms that lead to and influence invasion success.

128 In this contribution we explore such aspects using *Senecio inaequidens* DC. (Asteraceae),  
129 commonly called South African ragwort, as target species, with the aim to (1) assess the  
130 relative importance of abiotic and biotic factors in influencing the performance of *S.*  
131 *inaequidens*; (2) explore whether biotic resistance is determined by an interaction of both

132 factors; and (3) understand if biotic resistance to *S. inaequidens* is driven by diversity  
 133 levels or by similarity with resident plant species. Based on this we performed a field  
 134 survey in three different semi-natural habitats invaded by *S. inaequidens*, characterized by  
 135 different plant communities in terms of species composition and cover. We evaluated soil  
 136 characteristics, the resident vegetation structure of such habitats and the performance of  
 137 the invader. We hypothesize that an increase in diversity levels and/or similarity of the  
 138 resident species to *S. inaequidens* will decrease its performance, and that this effect would  
 139 be strengthened in more benign abiotic conditions (e.g., in conditions of higher soil nutrient  
 140 content).

141

## 142 **Methods**

### 143 *Target alien species*

144 *Senecio inaequidens* is a perennial chamaephyte native to South Africa. It can reach up to  
 145 100 cm in height, with hairless stems ending with yellow capitula arranging in irregular  
 146 cymose corymbs. It has linear petiole-less leaves irregularly dentate. The capitula are  
 147 formed by external ray- and internal disc flowers and the fruits are small achenes with  
 148 hairs between nerves and a white pappus, which favours dispersal of the seeds (Pignatti  
 149 2017). A single plant can produce up to 500-600 capitula each year, resulting in a  
 150 consistent number of achenes dispersed (up to 10.000-30.000) (Montagnani et al. 2018).  
 151 The plant's tissues contain pyrrolizidine alkaloids as a defence mechanism against above-  
 152 and belowground herbivory (Caño et al. 2009).

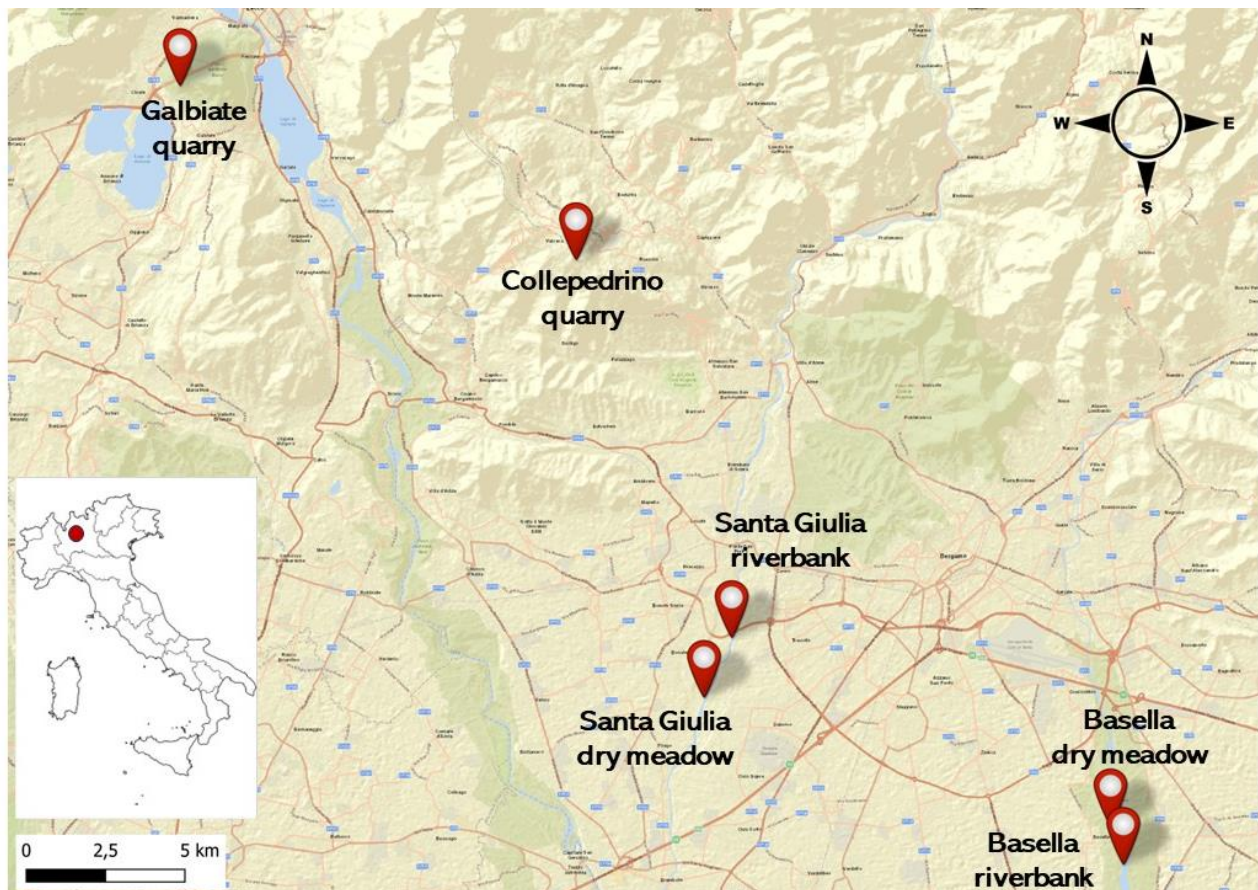
153 In South Africa, its native range falls in the inland plateau of Highveld where it grows at  
 154 high elevations (between 1400 and 2850 m a.s.l.) on skeletal sectors on steep and grassy  
 155 slopes, as well as sandy and gravelly riverbanks (Hilliard 1977; Ernst 1998; Heger and  
 156 Bohmer 2005). Its achenes were introduced to Europe by the end of the 19<sup>th</sup> Century as a  
 157 contaminant of sheep's wool, and from 1950 onwards the species started expanding  
 158 throughout Europe to other environments than the surroundings of wool industries (Ernst  
 159 1998). It is currently invasive to Europe and Mexico (Schmidt-Lebuhn et al. 2022). In Italy,  
 160 there are records of its presence in all the administrative regions, and it is invasive in  
 161 nearly most of them, where it generally grows in ruderal and stressed habitats, such as  
 162 along roadsides and trainlines, but also in crop fields, vineyards, rocky slopes, riverbanks,  
 163 meadows, and it can also colonize high-altitude pastures threatening flora and habitats of  
 164 conservation concern (Giunti et al. 2015; Montagnani et al., 2018). This species is

165 considered one of the fastest spreading invasive plant in Europe, especially in mountain  
166 systems (Vacchiano et al. 2013).

### 167 *Study area, sampling design and methods*

168 Field sampling took place in the administrative region of Lombardy, located in Northern  
169 Italy, which extends over a territory of about 24,000 km<sup>2</sup> and exhibits large landscape  
170 heterogeneity due to its geographical, geolithological, morphological, and climatic  
171 characteristics, as it extends from the Alps to the Po plain (Domenico 2001; Celesti-  
172 Grapow et al. 2009; Marchese et al. 2017). It is characterized by alpine/continental  
173 climate, with mean annual temperatures of 14°C and mean precipitations of 920 mm  
174 (calculated over the 1991-2020 period. ARPA Lombardia; <https://www.arpalombardia.it>).

175 Field surveys were performed in 2022 during summer. To explore different environments  
176 colonized by the target species as well as a gradient of biotic and abiotic factors, we  
177 selected 3 different semi-natural habitats where *S. inaequidens* is commonly found in its  
178 invasive range, characterized by different soil characteristics and plant communities.  
179 Namely, stony riverbanks, dry meadows, and grassy slopes of former quarries were  
180 investigated. In order to improve the representativeness of sampling, for each habitat type  
181 (hereafter named riverbanks, meadows, and quarries) we identified two different sites  
182 (total 6 sites: Santa Giulia and Basella riverbanks, along the Brembo and the Serio rivers  
183 respectively, Santa Giulia and Basella dry meadows, and Galbiate and Collepdrino  
184 quarries). In these sites, we sampled five 1x1 m plots (Bornkamm 2002) where the species  
185 occurred (N=30; Fig. 1; Tab. S1 of the Supplementary Materials).



186

187 Figure 1. Sampling sites. Sampling took place in the administrative region of Lombardy in  
 188 Northern Italy. We selected three different semi-natural habitats where *S. inaequidens*  
 189 commonly grows (stony riverbanks, dry meadows, and grassy slopes of former quarries),  
 190 and for each habitat type we selected two different sites (Santa Giulia and Basella  
 191 riverbanks, along the Brembo and the Serio rivers respectively, Santa Giulia and Basella  
 192 dry meadows, and Galbiate and Collepedrino quarries). In each site we sampled five plots  
 193 of 1x1 m (N=30) where the target alien species was present.

194 In each plot we collected approximately 150 g of soil to assess the nutrient content and  
 195 particle-size distribution. Soil samples were collected at a depth between 5 to 30 cm in  
 196 each plot; depth depended on habitat type, since, for example, riverbanks were  
 197 characterized by less developed soils, and therefore the plants grew on gravelly and sandy  
 198 material deposited by the river (Mologni 2015). Once collected, soil samples were air-dried  
 199 and sieved with a 2 mm mesh and stored at room temperature until analyses started.  
 200 Additionally, for each site in field, we visually estimated bare soil cover (expressed as  
 201 percentage of total cover not occupied by vegetation on the total plot area) and soil  
 202 surface stoniness, expressed as percentage of rock fragments (> 2 mm of diameter) on  
 203 the total plot area, as the proportion of rock fragments in soils can affect water availability  
 204 and the growth and physiological features of plants (Mi et al. 2016). To determine the  
 205 structure of the plant communities, we surveyed resident species present in each plot by  
 206 visually estimating their cover with the help of a gridded plot. We also evaluated *S.*

207 *inaequidens* performance by measuring its percentage cover and recorded some key  
208 functional traits which are known to reflect plant ecological strategies for resource  
209 acquisition, dispersal, establishment, and competitive ability (Westoby 1998): plant height  
210 (cm), specific leaf area (SLA;  $\text{mm}^2 \text{mg}^{-1}$ ) and flower production (n° of capitula).

#### 211 *Soil analyses*

212 Sieved soil samples were sent to the Geopedological Laboratory of the University of  
213 Milano-Bicocca to determine soil pH, available phosphorus (mg/kg), total nitrogen (%),  
214 organic carbon content (%), total carbonates (g/kg), and particle-size distribution (%). Total  
215 carbonates were assessed using a Dietrich-Fruhling calcimeter starting from 0.5-5 g of  
216 soil. Total carbon and nitrogen were measured using a CN elemental analyser (Flash EA  
217 1112 NC Soil, Thermo Fisher Scientific, Pittsburgh, USA). Organic carbon was then  
218 calculated as the difference between total carbon and total carbonates. Available  
219 phosphorus was extracted using sodium bicarbonate (Olsen et al. 1954). Soil particle-size  
220 distribution was additionally determined by sieving and sedimentation.

#### 221 *Phylogenetic metrics*

222 To calculate phylogenetic distances among species, including *S. inaequidens*, we  
223 constructed a phylogenetic tree comprising the 118 species found in our sampling sites. By  
224 means of the R package 'pez' (Pearse et al. 2015), we used a phylogenetic tree of all  
225 angiosperms as a backbone (Zanne et al. 2014) and removed all species that were not  
226 found in our sites (see Fig. S1 of the Supplementary Materials). We used the tree branch  
227 lengths to calculate phylogenetic distances in a matrix between pairs of species. From this  
228 matrix, we calculated the Community Weighted Mean Phylogenetic Distance (CWMPD),  
229 which is the mean distance between the target species (in this case, *S. inaequidens*) and  
230 the species of the resident communities (Thuiller et al. 2010), weighted by their cover.

231 To estimate phylogenetic diversity of resident plant communities, we calculated Faith's  
232 phylogenetic diversity (FaithPD) using the `pd()` function of the 'picante' R package (Kembel  
233 et al. 2010). Generally, higher PD values indicate communities that have more  
234 evolutionary divergent taxa and older history, while lower PD values are typical of  
235 assemblages that have taxa with more recent evolutionary history (Faith 1992; Swenson  
236 2014; El-Barougy et al., 2021).

#### 237 *Functional metrics*

238 Plant height of *S. inaequidens* individuals was measured in the field as the shortest  
239 distance between the upper boundary of the main photosynthetic tissue (excluding  
240 inflorescences) and the ground level (Pérez-Harguindeguy et al. 2013). Flower production  
241 (i.e., reproductive output) was recorded in the field counting the number of capitula (n° of  
242 capitula) per individual and considering buds, blooming heads, and drying heads (Caño et  
243 al. 2007). For determining SLA (i.e., the ratio of fresh leaf area to leaf dry mass,  
244 mm<sup>2</sup> mg<sup>-1</sup>), we collected 3 fresh leaves from the mid-stem of a single *S. inaequidens*  
245 individual of each plot and stored them in paper envelopes. In the laboratory, SLA was  
246 estimated by photographing each leaf collected, then subsequently drying them out at  
247 80°C till constant weight to be dry-weighted (Pérez-Harguindeguy et al. 2013). The area  
248 was calculated using the image analyses software ImageJ version 1.53 (Abràmoff et al.  
249 2004), and SLA was then calculated dividing the leaf area (mm<sup>2</sup>) by its dry weight (mg).  
250 SLA values for each individual of a plot was obtained by averaging SLA of the 3 leaves.  
251 To assess the functional structure of the invaded communities, we adopted the LHS (leaf-  
252 height-seed) scheme proposed by Westoby (1998), which effectively captures the diversity  
253 of plant ecological strategies concerning resource acquisition, dispersal, establishment,  
254 and competitive ability. Therefore, canopy height (cm), specific leaf area (SLA, mm<sup>2</sup>mg<sup>-1</sup>),  
255 and seed weight (mg) were selected as functional traits to characterize resident plant  
256 communities functionally. Information on such traits for the species in our plots were  
257 obtained from different available databases: LEDA (Kleyer et al. 2008), BioFlor (Kühn et  
258 al. 2004), the trait database published by Cerabolini et al. (2010), and the Seed  
259 Information Database (Liu et al. 2019). For some not frequent species (which accounted  
260 for <5% for the mean total plot cover in each site, i.e., *Anisantha rigida* (Roth) Hyl.,  
261 *Festuca geniculata* (L.) Lag. & Rodr., *Carex liparocarpos* Gaudin, *Ostrya carpinifolia*  
262 Scop.), none of the traits selected were available, so they were not included in the  
263 analyses. Prior to further statistical analyses, all trait measures were scaled by subtracting  
264 each value by its mean and dividing it by its standard deviation.  
265 We calculated the distance matrix between pair of species using Euclidean distances and  
266 we determined the functional distance of the invaded communities from *S. inaequidens* by  
267 calculating the Community Weighted Mean Functional Distance (CWMFD) (Thuiller et al.  
268 2010), that is the mean distance between the target species (*S. inaequidens*) and the  
269 species of the resident communities weighted by their cover.  
270 The selected traits (canopy height, SLA, and seed weight) for resident plant species were  
271 also used to quantify functional diversity of the invaded communities. We determined

272 functional richness (FRic), which is the amount of functional space filled with by the  
273 community, and functional dispersion (FDis), which calculates the distance of each  
274 species, weighted by their abundances, from the centroid of the community traits. These  
275 two metrics capture different aspect of functional diversity; while higher functional richness  
276 indicates a greater variety of traits and potential ecological roles within a community,  
277 higher functional dispersion suggests that species are more evenly distributed across the  
278 trait space, indicating a more even distribution of ecological strategies (Villéger et al.  
279 2008; Swenson 2014; El-Barougy et al. 2021). These metrics were calculated with the  
280 dbFD() function of the 'FD' package in R (Laliberté et al. 2014).

### 281 *Statistical analyses*

282 We first check for differences in the abiotic and biotic variables measured among the  
283 sampled habitats using the Kruskal-Wallis test for mean ranks (Kruskal and Wallis 1952).  
284 Dunn post-hoc test ('dunn.test' package in R (Dinno 2017)) was performed with Holm  
285 correction for multiple comparisons (Dunn 1961, Holm 1979).

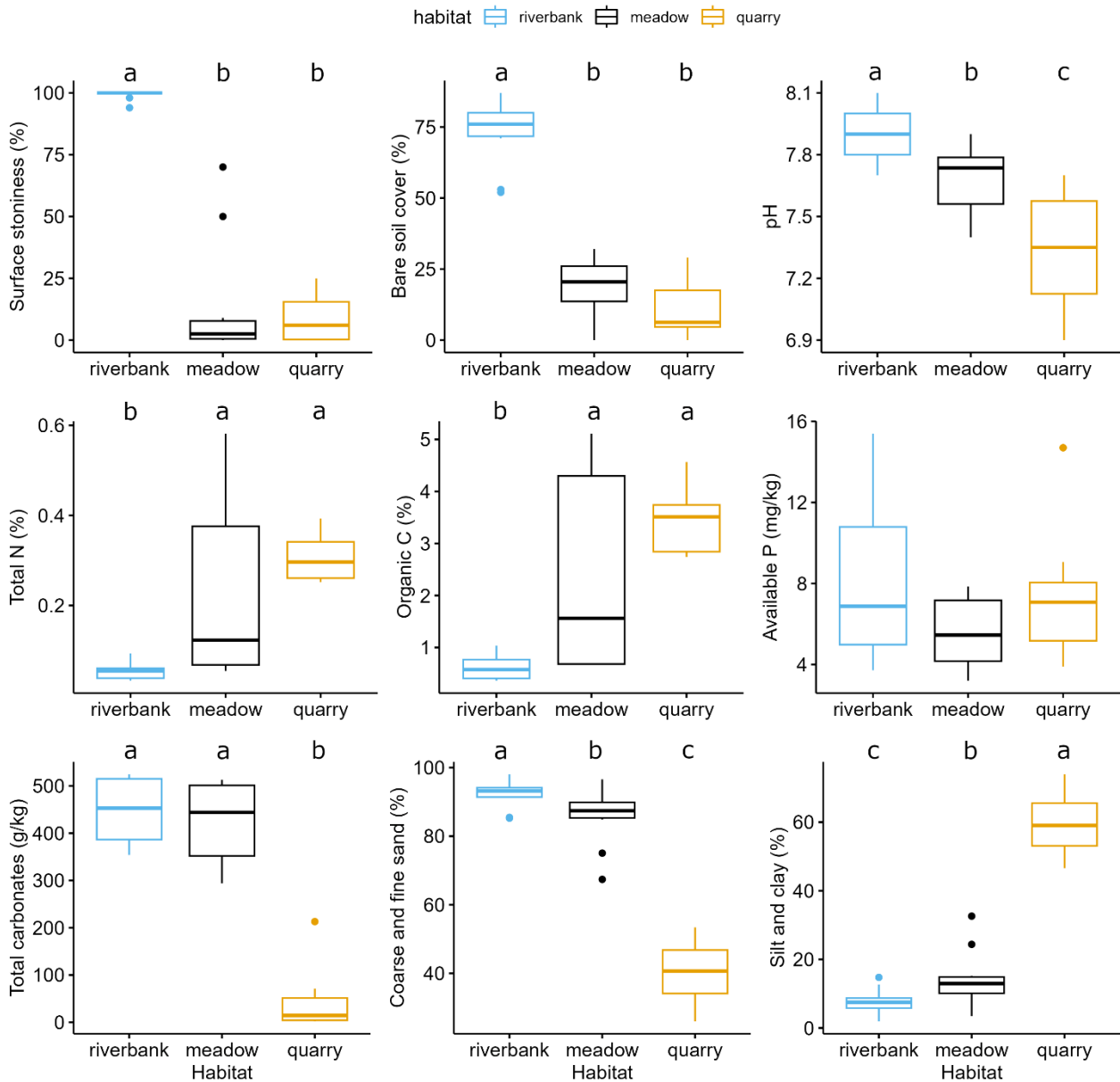
286 A final set of 14 variables (Tab. S2 of the Supplementary Materials) was used to build a  
287 series of generalized linear mixed models (GLMMs; glmmTMB() function of the 'glmmTMB'  
288 R package (Brooks et al. 2017)) to analyse the relationships between *S. inaequidens*  
289 performance and the abiotic and biotic conditions of the recipient environment. Variable  
290 selection was previously performed by removing highly correlated variables (one from  
291 each couple) when scored a Spearman's correlation index  $> 0.75$  (Gentili et al. 2020).

292 We first built univariate models, in which we included: (i) *S. inaequidens* performance  
293 (expressed as cover, canopy height, SLA and number of capitula) as response variable; (ii)  
294 abiotic (habitat identity, surface stoniness, soil total nitrogen, available phosphorus, sand  
295 fraction and silt-clay fraction) and biotic variables (proportion of alien species other than *S.*  
296 *inaequidens*, total resident species richness and cover (excluding *S. inaequidens*), Faith  
297 PD, FRic, FDis, CWMPD and CWMFD) as fixed factors; (iii) site as random factor. Then,  
298 we built multivariate models, in which we considered as fixed effects the 2-way interaction  
299 between those biotic variables which, in univariate LMMs, significantly affected *S.*  
300 *inaequidens* performance and all the abiotic variables, to assess whether the direction and  
301 strength of biotic interactions depend on the abiotic context. To model *S. inaequidens*  
302 cover we used beta distribution, for the n° of capitula we used negative binomial  
303 distribution, while for height and SLA, we used gaussian distribution. All statistical analyses  
304 were performed within the R environment v. 4.3.0 (R Core Team 2023).

305

306 **Results**307 *Habitat characterization*

308 Generally, in sampled plots, both biotic and abiotic factors varied among habitats (Fig. 2, 3;  
309 Tab. S3, S4 of the Supplementary Materials). Specifically, stony riverbanks represented  
310 the habitats with the highest levels of stoniness (hereafter mean  $\pm$  SD; Kruskal-Wallis  
311 results:  $99 \pm 0.02\%$ ;  $\chi^2=19.905$ ,  $P<0.001$ ), bare soil cover ( $73 \pm 0.12\%$ ;  $\chi^2=20.516$ ,  
312  $P<0.001$ ) and sand soil-fraction ( $92 \pm 0.04\%$ ;  $\chi^2=44.1446$ ,  $P<0.001$ ). Moreover, they  
313 showed the lowest values of organic carbon ( $0.6 \pm 0.23\%$ ;  $\chi^2=15.177$ ,  $P<0.001$ ) and total  
314 nitrogen ( $0.06 \pm 0.02\%$ ;  $\chi^2=16.075$ ,  $P<0.001$ ). Quarries, on the other hand, exhibited  
315 higher values of soil nutrients (organic C:  $3.43 \pm 0.61\%$ ; total N:  $0.31 \pm 0.05\%$ ) and higher  
316 contents of clay and silt ( $60 \pm 10\%$ ), compared to the other habitats sampled ( $8 \pm 3.5\%$  for  
317 riverbanks and  $14 \pm 9\%$  for dry meadows;  $\chi^2=44.2243$ ,  $P<0.001$ ). Dry meadows fell  
318 somehow into an intermediate situation between quarries and riverbanks sharing more  
319 similar characteristics with one or the other habitat type depending on the variable  
320 considered (e.g., dry meadows showed similar soil particle-size distribution as those found  
321 in riverbanks, but in terms of surface stoniness and bare soil cover, they were more like  
322 quarries; Fig. 2; Tab. S3 of the Supplementary Materials). pH values and total carbonates  
323 progressively declined from riverbanks to dry meadows and quarries ( $\chi^2=17.913$ ,  $P<0.001$ )  
324 but, in general, the substrate was alkaline in all habitats (the mean pH value for all tree  
325 habitats was  $7.63 \pm 0.31$ ). Levels of available phosphorus were similar among habitats  
326 (with a mean value of  $6.99 \pm 3.18$  mg/kg;  $\chi^2=3.3493$ ,  $P=0.1874$ ). Overall, stony riverbanks  
327 were characterized by the harshest abiotic conditions for plant growth, with low soil  
328 nutrients, high percentage of stoniness and the absence of a well-developed soil (Fig. 2;  
329 Tab. S3, S4 of the Supplementary Materials).

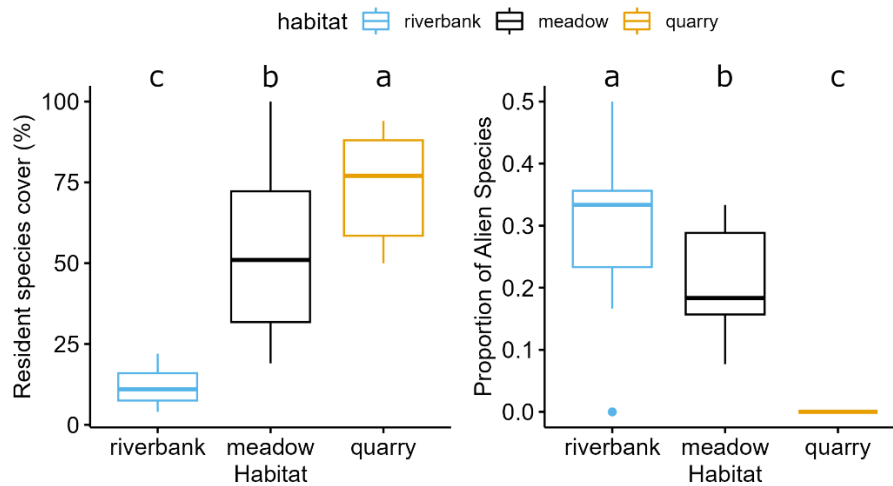


330

331 Figure 2. Differences in abiotic variables among sampled habitats. The boxplots display  
 332 the median values for abiotic variables measured in the three sampled habitats: stony  
 333 riverbanks (light blue boxes), dry meadows (black boxes) and grassy slopes of former  
 334 quarries (ocher boxes). Different lowercase letters indicate significant differences among  
 335 the habitats, determined with Kruskal-Wallis and Dunne post-hoc tests.

336 Most of the vegetation surveyed in the plots was herbaceous and accounted for a mean  
 337 value of 57.53% ( $\pm 31.1\%$ ) of the total plots cover (*i.e.*, considering both the vegetated area  
 338 and the bare soil cover), while the trees and shrubs layers together only accounted for an  
 339 average of 0.86% ( $\pm 2.6\%$ ). Moreover, while the different habitats hosted a similar number  
 340 of species (with a mean value of 8.83 ( $\pm 3.67$ ) species per plot ( $\chi^2=4.2349$ ,  $P=0.1203$ ), the  
 341 cover of the total resident vegetation significantly and progressively increased from

342 riverbanks to dry meadows to quarries ( $\chi^2=20.474$ ,  $P<0.001$ ). Interestingly, when  
 343 considering the presence of alien species other than *S. inaequidens*, we found an opposite  
 344 patten with regards to the total cover, with riverbanks that were characterized by the higher  
 345 proportion of aliens ( $\chi^2=19.989$ ,  $P<0.001$ ; Fig. 3; Tab. S4 of the Supplementary Materials).



346

347 Figure 3. Differences in resident species cover and alien proportion in the sampled  
 348 habitats. The boxplots display the median values the total residence species cover (%) on  
 349 the left, and proportion of alien species (other than *S. inaequidens*) on the right in the three  
 350 different sampled habitats: stony riverbanks (light blue boxes), dry meadows (black boxes)  
 351 and grassy slopes of former quarries (ochre boxes). Different lowercase letters indicate  
 352 significant differences among the habitats, determined with Kruskal-Wallis and Dunne  
 353 post-hoc tests.

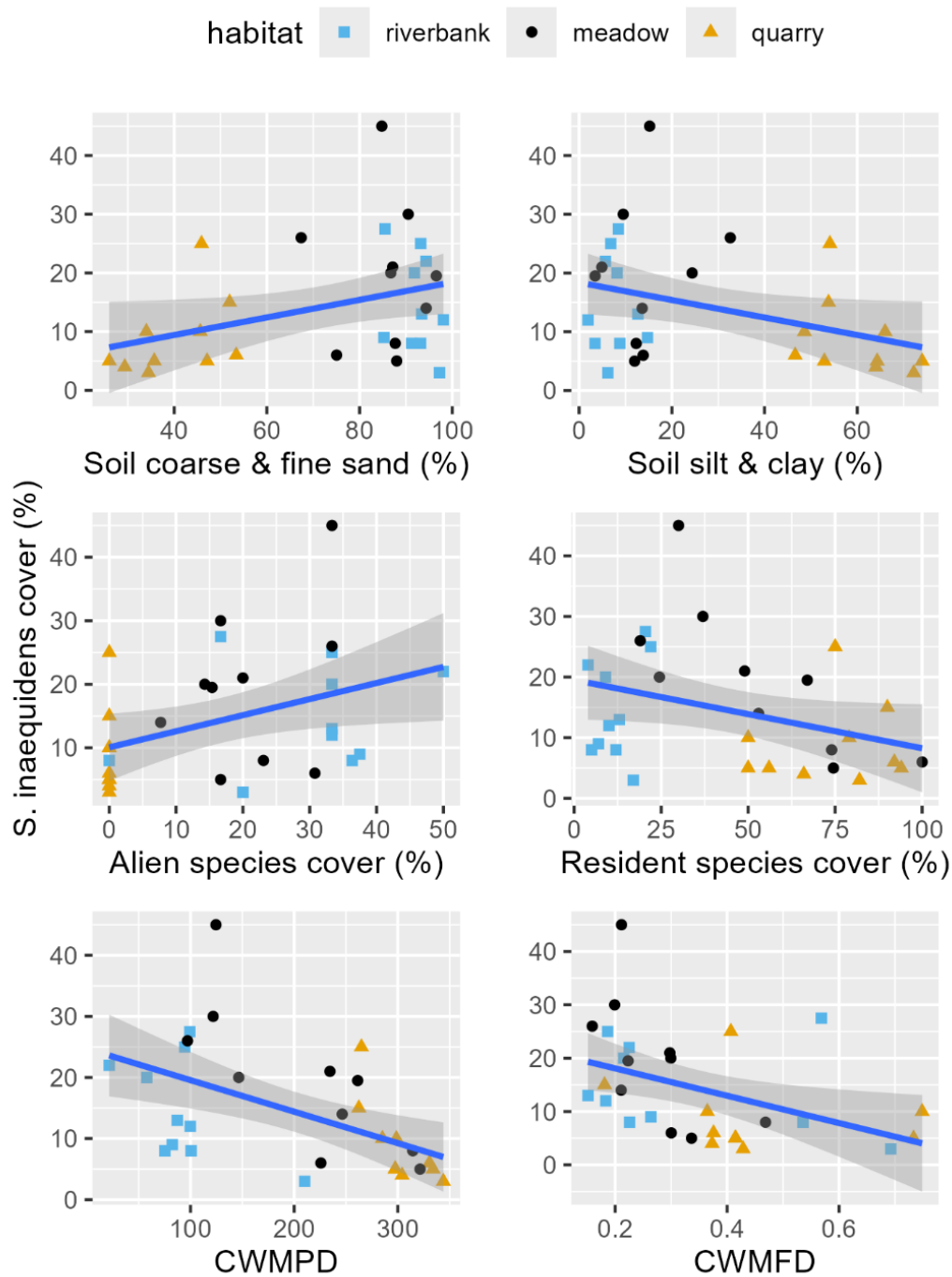
#### 354 *Influence of abiotic and biotic variables on S. inaequidens performance*

355 Overall, univariate GLMMs revealed a preponderance of biotic over abiotic factors in  
 356 affecting the target alien's performance (Tab. S5 of the Supplementary Materials). Soil  
 357 nutrient levels and particle-size distribution had marginal influence on the abundance and  
 358 the functional traits of *S. inaequidens*. Mainly, the cover of the target alien increased in  
 359 conditions of lower silt-clay and of higher sand content in soil (silt and clay:  $P=0.03$ ; sand:  
 360  $P=0.045$ ; Fig. 4). Soil total nitrogen content was associated with slight increased levels of  
 361 SLA ( $P=0.047$ ) and lower floral production ( $P=0.003$ ; Fig. 5). Moreover, *S. inaequidens*  
 362 showed and increased floral production in riverbanks habitats, in condition of higher  
 363 surface stoniness (respectively,  $P=0.005$  and  $P=0.002$ ; Fig. 5).

364 Regarding the biotic variables, they generally had a strong effect on the target species'  
 365 cover, height and floral production, while SLA (except for total nitrogen) was not affected  
 366 by any of the factors considered, whether they were biotic or abiotic (Tab. S5 of the  
 367 Supplementary Materials).

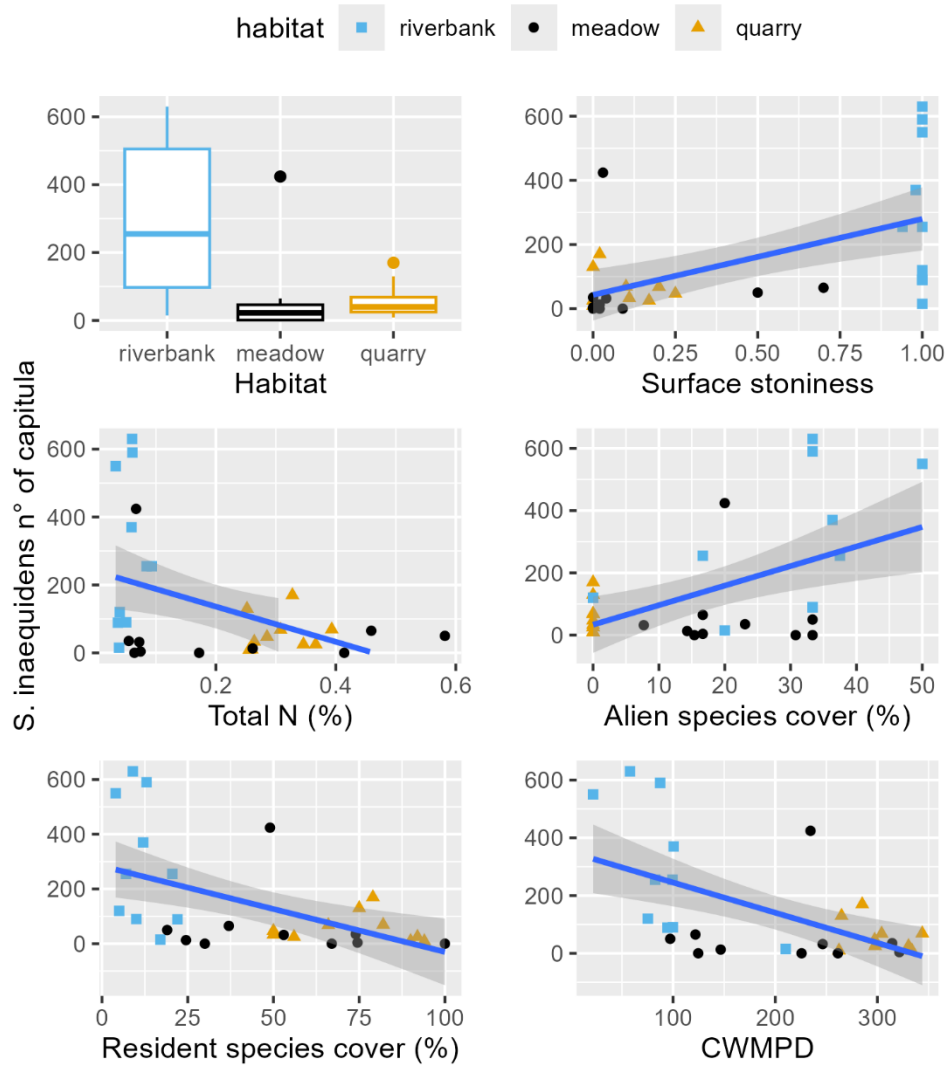
368 Cover and height of *S. inaequidens* revealed a negative relationship with plant  
369 communities' diversity measures such as species richness ( $P=0.08$ , for cover (near  
370 significance);  $P=0.02$  for height; Fig. 6) and Faith's PD ( $P=0.052$  for cover (near  
371 significance);  $P=0.05$  for height; Fig. 6). Yet, cover of *S. inaequidens* and all functional  
372 traits measured were not affected by the functional diversity measures considered (Tab.  
373 S5 of the Supplementary Materials). Our data also revealed that the total cover of the  
374 recipient plant species negatively influenced *S. inaequidens* performance ( $P=0.036$  for  
375 cover,  $P=0.0005$  for flower production; Fig. 4-5), and that its cover was positively  
376 associated with the proportion of other alien species present in the plots ( $P=0.021$  for  
377 cover;  $P=0.007$  for flower production; Fig. 4-5).

378 In terms of similarity patterns between *S. inaequidens* and the recipient communities, we  
379 found the target alien species cover and floral production to have a strong negative  
380 relationship with the weighted mean phylogenetic distance (CWMPD) to the recipient  
381 communities ( $P=0.02$  and  $P=0.0007$ , respectively; Fig. 4-5). A similar trend was also found  
382 for the functional distance (CWMFD), albeit with no effect on flower production (Tab. S5 of  
383 the Supplementary Materials), indicating to some degree a better performance of *S.*  
384 *inaequidens* cover when sharing high trait similarity with the recipient plant communities  
385 ( $P=0.0099$ ).



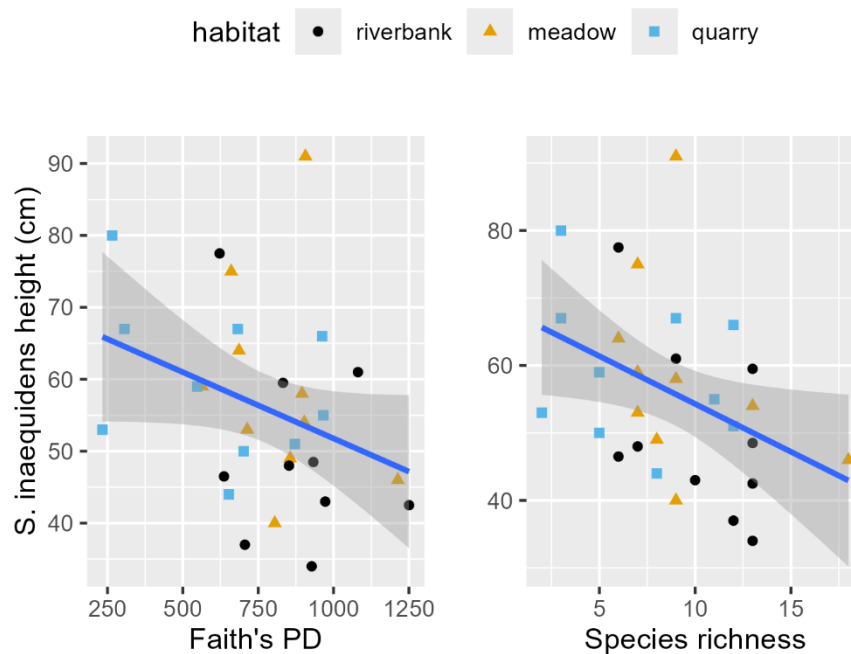
386

387 Figure 4. Results of GLMMs for *S. inaequidens* cover. In the panel are shown the  
 388 significant relationships found with GLMMs between *S. inaequidens* cover and (starting  
 389 from the left to the right, and from top to bottom): soil sand fraction ( $P=0.046$ ), soil silt and  
 390 clay fraction ( $P=0.034$ ), alien species cover (other than *S. inaequidens*;  $P=0.02$ ), resident  
 391 species cover (other than *S. inaequidens*;  $P=0.036$ ), CWMPD ( $P=0.022$ ), and CWMFD  
 392 ( $P=0.0099$ ). Light-blue squares represent riverbanks plots, black circle represent dry  
 393 meadows plots, and ochre triangles represent quarries plots. Random effect is site identity.



394

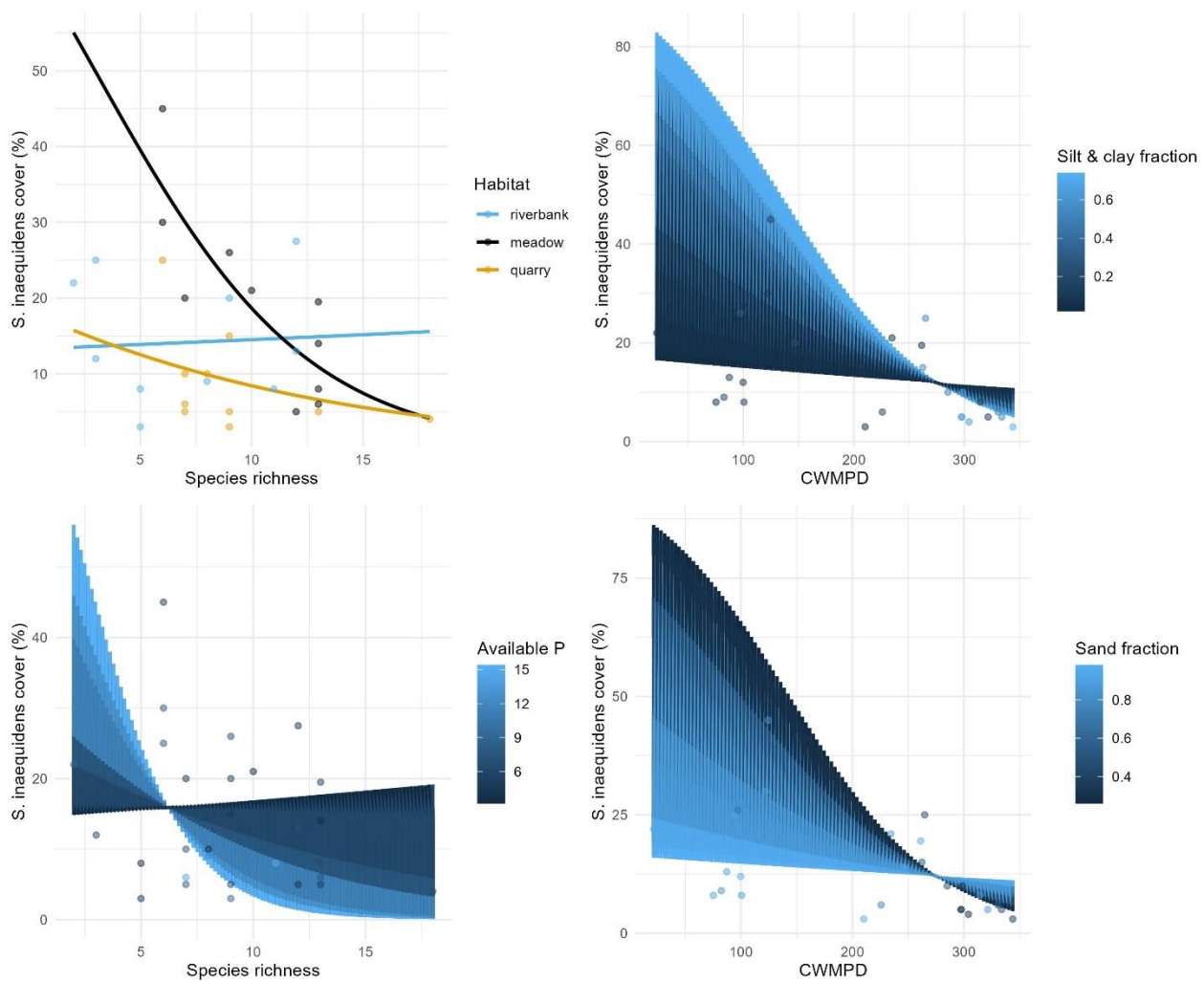
395 Figure 5. Results of GLMMs for *S. inaequidens* floral production. In the panel are shown  
 396 the significant relationships found with GLMMs between *S. inaequidens* n° of capitula and  
 397 (starting from the left to the right, and from top to bottom): habitat identity ( $P=0.0055$ ),  
 398 surface stoniness ( $P=0.0018$ ), total nitrogen ( $P=0.003$ ), alien species cover (other than *S.*  
 399 *inaequidens*;  $P=0.0065$ ), resident species cover (other than *S. inaequidens*;  $P=0.00045$ ),  
 400 and CWMPD ( $P=0.0007$ ). Light-blue squares represent riverbanks plots, black circle  
 401 represent dry meadows plots, and ochre triangles represent quarries plots. Random effect  
 402 is site identity.



403

404 Figure 6. Results of GLMMs for *S. inaequidens* height. In the panel are shown the  
 405 significant relationships found with GLMMs between *S. inaequidens* height and (starting  
 406 from the left to the right): FaithPD ( $P=0.05$ ), and species richness ( $P=0.0199$ ). Light-blue  
 407 squares represent riverbanks plots, black circle represent dry meadows plots, and ochre  
 408 triangles represent quarries plots. Random effect is site identity.

409 When analysing the two-way interactions between significant biotic variables and abiotic  
 410 ones, most of the interactions were non-significant (Tab. S6 of the Supplementary  
 411 Materials), except for species richness whose relationship with *S. inaequidens* cover  
 412 changed based on the habitat type ( $P=0.0031$ ) and on the phosphorus levels in soil  
 413 ( $P=0.0092$ ). In particular, there was a more negative relationship between the target alien  
 414 cover and resident species richness in dry meadows and quarries with respect to  
 415 riverbanks. This relationship is also more negative in conditions of higher phosphorus  
 416 content in soil (Fig. 7, Tab S6 of the Supplementary Materials). Similarly, we found a  
 417 significant interaction between CWMPD and soil particle-size distribution when modelled  
 418 with *S. inaequidens* cover (silt and clay:  $P=0.024$ ; sand:  $P=0.0163$ ). The relationship  
 419 between the cover of the alien and CWMPD was more negative in conditions of higher  
 420 content of finer soil particles (silt and clay) and of lower content of sand (Fig. 7).



421

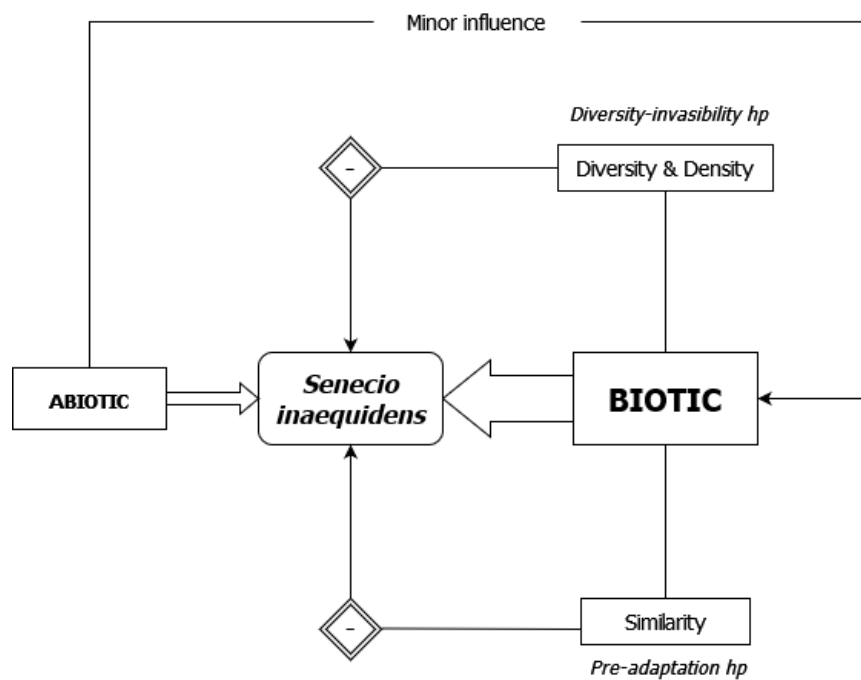
422 Figure 7. Two-way interactions between abiotic and biotic variables. The panel shows the  
 423 results of multivariate GLMMs with significant two-way interactions between the biotic and  
 424 abiotic variables; site identity is the random factor. In the plots on the left side of the panel,  
 425 we show how the relationship between *S. inaequidens* cover and species richness  
 426 changes in different habitats (top-left;  $P=0.0031$ ) and with different concentrations of  
 427 phosphorus in the soil (bottom-left;  $P=0.0092$ ). In the plots on the right side of the panel,  
 428 we show how the relationship between *S. inaequidens* cover and CWMPD changes based  
 429 on soil particle size distribution (top-right: silt and clay,  $P=0.024$ ; bottom-right: sand,  
 430  $P=0.06$ ).

431

## 432 Discussion

433 Our results highlighted that the overall performance of *S. inaequidens* was better  
 434 explained by the biotic interactions rather than the abiotic context. Considering that this  
 435 species is known for its ability to colonize a wide range of habitats, with different levels of  
 436 resource availability and harshness, these results suggest that *S. inaequidens* can tolerate  
 437 variations in abiotic conditions with marginal effects on its fitness (Heger and Bohmer

2005; Delory et al. 2019). Specifically, this alien plant seems to be more sensitive to biotic resistance driven mainly by resident communities' diversity, particularly in terms of competition for space, which can hinder its establishment (species cover and height) and fitness (reproductive output), giving support for the diversity-invasibility hypothesis (Fig. 8). However, when considering the similarity patterns between resident species and *S. inaequidens*, we found a contrasting result from what expected considering Darwin's naturalization and limiting similarity hypotheses, as our target species performed better when it was more similar to the resident communities, giving more support to the pre-adaptation hypothesis, especially considering that *S. inaequidens* is an extremely ruderal species that thrives in disturbed and stressed contexts, where the presence or the abundance of other plant species might be limited by abiotic conditions (Fig. 8).



449

Figure 8. Conceptual framework of the main results found in the present study. Biotic interactions had a greater effect on *S. inaequidens* performance than sites' abiotic conditions, and the latter had only a marginal effect on the strength and direction of biotic interactions between the target alien and the resident communities. We found evidence of biotic resistance of the resident communities when considering species diversity and density, giving support to the diversity-invasibility hypothesis. However, when considering the similarity pattern between *S. inaequidens* and the resident plant species, we found support for the pre-adaptation hypothesis, and not to the Darwin's naturalization/limiting similarity hypotheses, as *S. inaequidens* performed better when more similar to the communities invaded.

In terms of the effects of abiotic variables, we found *S. inaequidens* SLA to have a marginal positive response to increasing values of soil nitrogen; floral production, instead,

462 appeared to be positively related to increasing values of stoniness, while its cover was  
463 positively associated to higher levels of sand content in soil and lower silt and clay. Our  
464 results did not completely reflect previous studies that found introduced populations of *S.*  
465 *inaequidens* to respond to increased resource availability by increasing its biomass and  
466 reproductive output (Bossdorf et al. 2008). The fact that we found a higher number of  
467 capitula along stony riverbanks, characterized by the harshest environmental conditions  
468 (i.e., high surface stoniness, low soil nutrient content, high content of sand), and denser  
469 populations in conditions of higher sand contents in soil, indicates the species higher  
470 ability to cope with disturbed and stressful environments in comparison to other species of  
471 the resident community (Garcia-Serrano et al. 2009; Delory et al. 2019). In these stressful  
472 environments, it is likely that the reproductive efforts of the species at the individual level  
473 needs to be increased to have more possibilities of establishment. In fact, here vegetation  
474 cover of the recipient community was at the lowest level compared to the other habitats  
475 sampled. In contrast, quarries, characterized by elevated levels of soil nutrients and  
476 silt/clay content, generally showed lower cover of *S. inaequidens* and higher of resident  
477 plants', likely indicating a more competitive environment (Damgaard 2011). *S. inaequidens*  
478 is a known early-successional ruderal species that requires open spaces with low  
479 competitive pressure to establish, and that's the reason why it thrives in stressed and  
480 disturbed sites, where competition with other plant species is thought to be less important  
481 (Heger & Bohmer 2005; Delory et al. 2019; this study). Indeed, it has been observed that  
482 this species has difficulties in establishing if native vegetation has already relevant cover  
483 values in a site. It is likely one of the first arriving species in open and stony areas (Delory  
484 et al. 2019). Already established and dense plant communities are unlikely to be invaded  
485 by *S. inaequidens* (Delory et al. 2019), but if a disturbance leads to a significant reduction  
486 of native plant cover, it's first appearance before other species could potentially lead to  
487 invasion (Ernst 1998; López-García and Maillet 2005).

488 In support with the diversity-invasibility hypothesis, we found *S. inaequidens* performance  
489 to negatively respond to higher species richness and, marginally, to higher phylogenetic  
490 diversity of the recipient communities. However, these patterns were partially contingent to  
491 the habitat sampled, with recipient community's richness showing almost no effects in  
492 riverbanks, and likely modulated by resident species cover and phosphorus content.  
493 Therefore, our results support the idea that recipient communities with high diversity  
494 and/or abundance of species generally offer fewer opportunities for the establishment of  
495 potential invaders, due to the scarcity of available resources such as nutrients and light

496 (Lindig-Cisneros and Zedler 2002; Byun et al. 2015). The same patterns were not reflected  
497 when considering functional diversity, which could be explained by the fact that we only  
498 considered a limited number of traits that might have not been relevant for assessing  
499 functional diversity of the sampled communities (Funk et al. 2017; Ernst et al. 2022).

500 Contrary to our expectations, we found a strong negative relationship between both the  
501 high functional and phylogenetic distance and the performance of *S. inaequidens*.  
502 Specifically, our data showed the target alien to perform better in communities containing  
503 more functionally similar and closely related species. Such results are in contrast with what  
504 predicted by Darwin's naturalization and limiting similarity hypotheses. Conversely, our  
505 results support what is known as the pre-adaptation hypothesis, which suggests that alien  
506 species closely related (or functionally similar) to natives may share traits that allow them  
507 to adapt to the same environmental conditions (Ricciardi and Mottiar 2006; Ma et al.  
508 2016). These two seemingly contrasting and co-existing hypotheses are considered in the  
509 so-called 'Darwin's naturalization conundrum' (Diez et al. 2008; Thuiller et al. 2010), and  
510 have been posed to be contextually modulated by the relative importance of habitat  
511 filtering and competitive interactions (Fan et al. 2023). For instance, a recent study found  
512 patterns in invader-resident species phylogenetic distances at the community level to vary  
513 according to functional groups considered, resource and stress gradients (Wang et al.  
514 2024). Specifically, Wang et al. (2024) observed a strong negative effect of phylogenetic  
515 similarity on invader cover in plots experiencing resource scarcity, depending on the  
516 functional groups considered and particularly related to light and water availability. Such  
517 context dependency is also confirmed in our study where we find abiotic context to  
518 determine the strength of *S. inaequidens* response to phylogenetic similarity to the  
519 recipient community via abiotic conditions.

520 Nevertheless, when analysing the interactions between abiotic and biotic variables, we  
521 found only a marginal confirmation of our initial hypothesis, as we detected an influence of  
522 some abiotic characteristics on the relationship between species richness and the target  
523 alien's abundance. In harsh conditions (i.e., in stony and sandy soils with low nutrient  
524 content) this relationship was less negative, while in more favourable environments (i.e., in  
525 soils with higher contents of the finer soil fractions and nutrient levels), it was significantly  
526 more negative, thus suggesting stronger biotic resistance in more benign environmental  
527 conditions. But this pattern was observed only for a very limited number of the  
528 environmental variables considered (i.e., along riverbanks and with less phosphorus  
529 available in the soil). Though limited, these results are in line with those of several

530 previous studies revealing the role of abiotic factors in shaping the direction of biotic  
531 interactions (see e.g., Fried et al. 2018; El-Barougy et al. 2021; Byun et al. 2022). El  
532 Barougy et al. (2020), for instance, observed in an arid land that alien plants tend to co-  
533 exist with natives that are functionally dissimilar in richer and more favourable  
534 environmental conditions, likely because of a divergence in resource-use strategies. On  
535 the contrary in more harsh and extreme situations, aliens and natives were observed to be  
536 more functionally similar, because under stressful conditions they would likely share  
537 analogous simultaneous response to the limiting environmental resources (El Barougy et  
538 al. 2020). Similarly, (Fried et al. 2018) found that the invasive *Humulus japonicus* was  
539 more successful and showed more plasticity than a native co-occurring species only under  
540 conditions of higher resource availability, while in conditions of low resources it lost its  
541 advantage. The observed influence of soil phosphorus in modulating the effects of species  
542 richness on *S. inaequidens* cover can be attributed to the likelihood that higher  
543 phosphorus concentrations increasing the competitive ability of resident species, thus  
544 enhancing biotic resistance. A similar finding was reported by Byun et al. (2022), who  
545 observed in a pot experiment that soil nutrient levels did not directly impact the  
546 performance of the invasive *Sicyos angulatus*, but indirectly affected biotic resistance  
547 through the competing native species performance.

548

## 549 **Conclusions**

550 Our results confirm the notion that *S. inaequidens* is more susceptible to competition  
551 rather than adverse abiotic conditions, making it a good colonizing species rather than a  
552 strong competitor (Scherber et al. 2003; Caño et al. 2007; Thébault et al. 2011; Van De  
553 Walle et al. 2022). This also implies that in ruderal or stressed environments being  
554 functionally similar to the recipient community's species could confer *S. inaequidens* an  
555 advantage to invade. Therefore, our results also highlight the importance of biotic  
556 resistance through higher functional diversity in preventing this target alien's performance.  
557 However, considering the similarity patterns between resident species and *S. inaequidens*,  
558 we found that sharing similar strategies to the recipient community species can facilitate its  
559 invasion in disturbed and stressful contexts, where the presence or the abundance of other  
560 plant species might be limited by abiotic conditions. While some abiotic characteristics  
561 influenced the relationship between species richness and the target alien's abundance,  
562 particularly in harsh and favourable environments, this effect was limited. These findings

563 align with previous studies showing abiotic factors shaping biotic interactions, suggesting a  
564 nuanced interplay between environmental conditions and invasion dynamics.

565

## 566 **Acknowledgements**

567 We heartily thank Davide Abu El Khair and Arianna Comotti for the precious help during the  
568 field work; Davide Abu El Khair and Fabio Moia for assisting us with the soil analyses, and  
569 the two anonymous reviewers for their corrections and useful comments on how to  
570 improve the manuscript. This research was founded by the University of Milano-Bicocca.  
571 FY acknowledges the Alexander von Humboldt Foundation's support through the Feodor  
572 Lynnen Research Fellowship.

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