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This is a pre print version of the following article:

Original Citation:

Availability:

This version is available <http://hdl.handle.net/2318/1622631> since 2017-01-20T11:50:47Z

Published version:

DOI:10.1007/s11258-012-0130-5

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(Article begins on next page)

This is the author's final version of the contribution published as:

[Castagneri D., Garbarino M., Nola P. 2013. Host preference and growth patterns of ivy (*Hedera helix* L.) in a temperate alluvial forest. *Plant Ecology* 214: 1-9. ISSN: 1573-5052, doi: 10.1007/s11258-012-0130-5.]

The publisher's version is available at:

[<http://link.springer.com/article/10.1007/s11258-012-0130-5>]

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1 **Host preference and growth patterns of ivy (*Hedera helix* L.) in a temperate alluvial forest**

2

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18 Word count including all text (abstract, body of the text, and references): 5821

19

20 Keywords: competition, liana, plain forest, ring width

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27 **ABSTRACT**

28

29 Recent studies have highlighted the role of lianas in shaping stand dynamics both in tropical and
30 temperate forests. However, English ivy (*Hedera helix* L.), one of the most widespread liana in
31 Europe, has received little attention. We conducted a study in the Siro Negri alluvial forest (NW
32 Italy) to determine what factors most affected ivy distribution, and to investigate its interactions
33 with the trees in the stand. We evaluated the influence of tree size, age, species and neighborhood
34 crowding on ivy occurrence. In addition, growth ring widths were used to explore the development
35 pattern of climbing stems.

36 Fifty-two percent of trees in our study plots carried ivy, a value comparable to liana incidence found
37 in mature tropical forests. Tree characteristics and their spatial pattern significantly influenced ivy
38 distribution. Preferred hosts were large, isolated trees, while the effect of tree age and species on ivy
39 occurrence was marginal. Growth pattern analysis revealed that radial growth was positively related
40 to the available space on the tree trunk for each ivy stem. We conclude that neighborhood crowding
41 around trees and competition among climbing stems relying on the same trunk may reduce the
42 colonization rate of ivy.

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53 **INTRODUCTION**

54

55 Lianas are woody climbing plants that begin their life as terrestrial seedlings and later ascend to the
56 canopy using trees as structural supports (Putz and Mooney 1991). Over the past few years their
57 importance in forest biodiversity has been recognized (Schnitzer and Bongers 2002): they increase
58 woody species diversity and provide food and refuge for many animal species (Emmons and Gentry
59 1983; Campanello et al. 2007; Page et al 2010). Lianas play a central role in forest dynamics, as
60 they can suppress tree regeneration, and they compete with adult trees for light, water, and soil
61 nutrients. In some cases they have been found to reduce tree growth rates and fecundity (Ladwig
62 and Meiners 2010a; Ichihashi and Tateno 2011). Moreover, abundant lianas increase crown
63 susceptibility to wind and, in temperate climates, to snow damage (Allen et al. 2005). Lianas can
64 also influence forest composition, as they affect tree species differentially, modifying inter-specific
65 relationships. Furthermore, lianas can occupy available space on the ground earlier than pioneer tree
66 species, delaying gap colonization and forest succession (Laurence et al. 2001; Schnitzer and
67 Bongers 2002; Toledo-Aceves and Swaine 2008).

68 Since lianas have such an important role in forest dynamics, research on their distribution, ecology
69 and relationships with other plants is critical. Several studies have investigated liana dynamics at
70 stand level, revealing that abiotic factors, forest structure and stand dynamics influence their
71 distribution (Laurence et al. 2001; Allen et al. 2005; Londrè and Schnitzer 2006; Morrissey et al.
72 2009; Gianoli et al. 2010; Macía 2011; Nogueira et al. 2011). Few studies have taken an individual
73 tree approach to tree liana-tree relationships, and there is little information on how lianas interact
74 with their hosts, especially for temperate forests (Blick and Burns 2011; Ichihashi and Tateno
75 2011). As structural parasites, lianas need suitable supports to reach the canopy and maintain
76 themselves there. As a consequence, host tree characteristics, such as size and species, influence
77 lianas colonization patterns, growth rates, distribution and diversity (Leicht-Young et al. 2010;
78 Nogueira et al. 2011).

79 At a global scale, lianas are widespread in tropical forests, where they represent between 10 and
80 40% of the woody species (Schnitzer and Bongers 2002), but they are even common in several
81 temperate ecosystems. In Europe, there are few autochthon liana species, and white vine (*Clematis*
82 *vitalba* L.), grapevine (*Vitis* spp.) and English ivy (*Hedera helix* L.) are the most diffuse. The genus
83 *Hedera* originated in the Tertiary, experiencing a postglacial re-colonization from the
84 Mediterranean regions. As ivy belongs to a largely tropical family (Araliaceae), it benefits from
85 warm summers, and is intolerant to cold temperatures (Metcalf 2005). It favours nutrient-rich and
86 moist soils. Unlike many of the woody species found in southern-European plain forests, ivy is an
87 evergreen species. It presents two distinct forms: the chamephyte form at the beginning of its life,
88 with prostrate, sterile stems and palmately-lobed shade leaves that can create extensive carpets on
89 the forest floor; and the phanerophyte form when suitable supports are available and ivy stems can
90 ascend toward better light conditions. The climbing stems support reproductive shoots, with
91 unlobed oval sun leaves (Nola 1997; Garfi and Ficarrota 2003; Metcalfe 2005). Like other lianas,
92 ivy is a serious concern for forest managers. Despite its contribution to biodiversity maintenance
93 and to nutrient cycling processes (Badre et al. 1998), ivy is often regarded as a problem, as it is
94 believed to reduce tree growth rates. Moreover, outside of its natural distribution areas, ivy is an
95 invasive species that poses a grave threat to native plants (Clarke et al. 2006; Biggerstaff and Beck
96 2007), and active management is required to control it.

97 Despite its wide home range, extending from southern Scandinavia to the Mediterranean area, few
98 studies have been conducted on ivy dynamics, and those mainly in the Rhine valley, France
99 (Trèmollières et al. 1988; Schnitzler 1995; Badre et al. 1998; Schnitzler and Heuzè 2006; Heuzè et
100 al. 2009). Research on other species can be only partially transposed to ivy, as morphological and
101 ecological features vary between liana species (Gianoli et al. 2010).

102 We conducted a study in the Siro Negri forest, one of the very few fragments in northern Italy of
103 alluvial forest, a preferential habitat for this species (Schnitzler and Heuzè 2006). Our general
104 purpose was to explore ivy dynamics on an individual tree basis. The first goal was to quantify ivy

105 abundance in the forest, as quantitative assessments of lianas in Europe are extremely scarce.
106 Subsequent analyses were conducted to study individual ivy-host relationships. We aimed at
107 identifying the characteristics of preferred host trees, such as size, age, species, and neighborhood
108 crowding, in order to better understand which factors affect ivy occurrence. We then explored the
109 relationships between ivy radial growth rates and host tree characteristics, to obtain information on
110 ivy development following host ascension.

111

112 **METHODS**

113

114 **Study site**

115 The study was conducted within the Siro Negri Reserve, on the southern side of the Ticino Regional
116 Park, province of Pavia, northern Italy (45°12'N, 9°03'E, 65 m a.s.l.). Mean annual rainfall is about
117 800 mm, with most precipitation in spring and autumn, and the average annual temperature is 13.6
118 °C (Pavia weather station, 10 km from the study site). The forested area, described as a *Polygonato*
119 *multiflori-Quercetum roboris* association (Sartori 1984), covers about 9 ha, and is one of very few
120 relicts of the original alluvial forest in northern Italy. The main tree species are *Acer campestre* L.,
121 *Carpinus betulus* L., *Crataegus monogyna* Jacq., *Populus alba* L., *Populus nigra* L., *Quercus robur*
122 L., *Robinia pseudacacia* L., *Ulmus minor* Mill. The forest accommodates trees of over 100 years.
123 The last important human disturbances coincide with the two world wars, when there was an
124 elevated demand for firewood (Motta et al. 2009), while the forest has been unmanaged since the
125 establishment of the reserve in 1970.

126

127 **Field sampling**

128 Two permanent plots (50 × 50 m) were established during 2005 at the south-eastern border of the
129 reserve (Motta et al. 2009). Two other permanent plots (60 × 60 m) were established at less than
130 100 m of distance in the inner part of the reserve during 2009. Trees with diameter at breast height

131 (DBH) \geq 7.5 cm were identified, labeled with numbered plastic tags and mapped. All trees in the
132 reserve were mapped between 2009 and 2011.
133 During 2011, tagged trees in the four permanent plots (total area equal to 1.22 ha) were re-surveyed,
134 and a census of ivy was carried out. For each tree, we measured the diameter of living ivy stems \geq
135 0.5 cm at 1.3 m from the base. All the stems were measured without distinguishing between ramets
136 and genets, because it was difficult to identify their origin, and their dynamics and effects on trees
137 are comparable (Gerwing et al. 2006; Schnitzer et al. 2006; Campanello et al. 2007). The degree of
138 ivy occupancy on trees was classified according to a five class system: 0, ivy absent or below 1.3 m
139 on the tree trunk; 1, ivy present on the lower half of the trunk; 2, ivy reaching the second half of the
140 trunk, but not the crown; 3, ivy on the lower part of the principal branches; 4, ivy covering the
141 whole crown.

142

143 **Dendrochronological analysis**

144 An increment core from all the trees with DBH \geq 10 cm and from a subsample of trees with DBH <
145 10 cm was taken at 50 cm from the tree base. In addition, an increment core was taken at 50 cm
146 from the tree base from 60 randomly chosen ivy stems in the plots. The stems were cored from side
147 to side to get a core with two radii, in order to account for possible asymmetrical growth of ivy
148 stems. In the laboratory, all the cores were fixed to wooden supports and prepared with a razor to
149 obtain an optimal surface resolution.

150 Cores from trees were used to estimate tree age. For cores that did not intersect the pith, its position
151 was estimated by means of a pith locator, and the number of missing rings was estimated (Motta
152 and Nola 2001). When it was not possible to estimate missing rings, the core was discarded.

153 Ring widths of ivy cores were measured to the nearest 0.01 mm, using LINTAB device and
154 CATRAS software (Aniol 1983). Cores with rotten wood or other irregularities were discarded.

155 Cores were also discarded when the two series of radii for each did not match (visual comparison).

156 Series from the two radii of each of the remaining 43 cores (28.3% discarded) were averaged to
157 estimate annual stem growth rate.

158

159 **Data analysis**

160 The relationships between ivy and trees were explored on an individual tree basis. Descriptors of
161 ivy, computed for each host tree, were number of stems, diameter sum, basal area, diameter of the
162 largest stem, and the degree of ivy occupancy. Tree features were diameter, age (when available),
163 and species. Also, to analyze the effects of neighborhood crowding on ivy-tree interactions, we
164 calculated the number and the sum of diameters of trees in a circle of 10 m around the tree; and the
165 neighborhood ratio calculated as the ratio between the sum of neighbors' diameters and the subject
166 tree diameter (Daniels et al. 1986; Castagneri et al. 2008). A radius of 10 m was selected because
167 the largest trees in the stand have a crown radius > 8 m, thus they compete with trees at a distance
168 of more than 8 meters.

169 Firstly, we ran all the variables in a Redundancy analysis (RDA), to order ivy attributes in relation
170 to tree and neighborhood characteristics. RDA was done on Canoco 4.0 software (Ter Braak and
171 Smilauer 1998) and the statistical significance of the relations between variables was tested by a
172 Monte Carlo test with 10,000 permutations. Next, to refine the assessment of ivy-tree interaction,
173 we performed two types of models: (1) binary logistic regression models to evaluate the
174 characteristics that determined the presence/absence of ivy on a tree, with stepwise entry of
175 predictor variables (tree characteristics and neighborhood measures); (2) General Linear Models
176 (GLMs) to determine which factors influenced ivy abundance on host trees, again, via stepwise
177 entry of predictor variables (tree characteristics and neighborhood measures). In this case, response
178 variables were number of ivy stems on the tree, sum of stem diameters, and their basal area. When
179 continuous variables were not normally distributed, a transformation was applied to improve
180 linearity of relationships. Variable collinearity and distribution of the residual were checked for
181 each model. Finally, we analyzed ivy growth rate in relation to tree characteristics, neighborhood

182 crowding and ivy abundance. Individual growth rate, which was the response variable, was
183 calculated as mean radial increment during the last 5 and 10 years, obtained from the ivy cores. All
184 models were computed using SPSS 17.0 (SPSS Inc. Chicago IL).

185

186 **RESULTS**

187

188 **Ivy distribution**

189 Ivy density in the Bosco Negri alluvial forest was 657, 346 and 225 stems per hectare considering
190 stems of respectively ≥ 0.5 , 1 and 2.5 cm (three diameter thresholds commonly used in liana
191 censuses, Gerwing et al. 2006). The basal area of stems ≥ 0.5 cm was 5609 cm² per hectare. Of the
192 surveyed trees (n = 374), 52% hosted one or more ivy stems, although ivy was found only on the
193 tree trunk in many cases, and just 17% of the trees had ivy at crown level (classes of occupancy 3
194 and 4). Other liana species (*Clematis vitalba* L., *Vitis* spp.) occurred sporadically (0-2 individuals
195 per plot).

196 A few differences were observed between the four plots. Plot 3, characterized by low tree density
197 and large diameters, had the highest percentage of trees hosting ivy (Table 1), the largest number of
198 ivy stems larger than 0.5 cm (Fig. 1), and the largest ivy basal area (Fig. 2). Like Plot 3, Plot 4 was
199 located in the inner part of the reserve, but had a higher tree density and a lower mean diameter. It
200 had fewer ivy stems ≥ 0.5 cm, while the number of stems ≥ 2.5 cm was close to that in Plot 3. Plots
201 1 and 2, located at the forest border, had a much higher tree density. The percentage of trees hosting
202 ivy, the density of stems ≥ 1 and 2.5 cm, and ivy basal area were rather similar to those observed in
203 Plot 4, whereas the number of stems ≥ 0.5 was greater (Fig. 1).

204

205 **Ivy-tree relationships**

206 RDA highlighted the complexity of relationships between ivy and trees attributes. In the first
207 analysis (Fig. 3a) we included the descriptors of ivy, tree and neighborhood but not tree age for

208 each of the 374 sampled trees. In the second analysis (Fig. 3b) we included age as a variable. As
209 this information was not available for all the trees, the second RDA was performed on a sub-set of
210 207 samples. Relationships between variables were statistically significant ($p < 0.001$) in both the
211 RDA analyses, and the models explained 43.8% and 44.1% of variance respectively.

212 The ivy descriptors *HE_ba*, *HE_s_d*, *HE_d_M*, *HE_n* and *HE_cl* expressed liana abundance on
213 trees in different ways, and they were positively associated to each other. With regards to ivy-host
214 interactions, while tree diameter (*TR_d*) and age (*TR_age*) were positively related to ivy descriptors,
215 neighborhood crowding (expressed as neighbors number (*NE_n*), sum of diameters (*NE_s_d*), and
216 neighborhood ratio (*NE_ra*)) were negatively related to ivy abundance. In terms of species, RDA
217 showed that *Q. robur* trees were big and isolated, hosting large amounts of ivy whereas *A.*
218 *campestre* and *C. monogyna* trees were small with many neighbors, and hosted little ivy. The other
219 species were in an intermediate position. The inclusion of plot as a factor did not significantly
220 improve RDA (the variance explained by the model was 44.3%, graph not shown), suggesting that
221 the observed relationships were not influenced by site characteristics. RDA provided a general
222 pattern of ivy-host relationships. However, it was not possible to identify which tree characteristics
223 were most important in favoring ivy, as many variables correlated with each other. To discriminate
224 between these factors, several models were applied. The logistic regression model showed that the
225 presence of ivy was positively related to big tree diameters and negatively related to the number of
226 neighboring trees (Table 2), indicating that larger isolated trees were more likely to host ivy than
227 the others. Tree species increased the Nagelkerke R^2 from 0.276 to 0.303, but was not significant at
228 $p = 0.05$. Tree age was positively related to ivy, while the sum of diameters of neighbors and
229 neighborhood ratio correlated negatively, but these factors were discarded as redundant in the
230 stepwise regression. Including plot as a factor did not improve the model, indicating that the
231 observed patterns did not vary significantly between the four plots.

232 To determine which characteristics of host trees ($n = 194$) influenced the amount of ivy, we looked
233 at the number of ivy stems per tree, and their sum of diameters and basal area. These direct

234 measurements of ivy abundance correlated more closely to tree descriptors than diameter of the
235 biggest stem and tree occupancy category. GLMs indicated that abundance of ivy was influenced by
236 the same factors that determined its presence. Tree diameter was the most important feature,
237 positively influencing ivy abundance, while the number of neighbors had a negative effect (Table
238 3). Tree species emerged as a significant factor only in predicting ivy stem number, with *Q. robur*
239 and, more evidently, *C. monogyna*, hosting fewer stems than the other species. The best model
240 performed similarly in predicting the number of ivy stems on the tree and their sum of diameters,
241 while it explained a lower percentage of variance for ivy basal area.

242

243 **Ivy growth patterns**

244 The largest sampled ivy stem had a diameter of 14 cm at 50 cm from the base, and 53 counted rings,
245 while the oldest one had 69 rings, and a diameter of 9.5 cm. Five stems had an estimated age > 50
246 years. The mean annual radial growth rate was 1.05 (\pm 0.54) mm over the last five years, and 1.03
247 (\pm 0.47) mm over the last ten years. Relationships between host tree characteristics and ivy growth
248 were rather weak, and only host tree age was positively related to the rate of growth over the last ten
249 years (Pearson's $r = 0.36$, $p < 0.05$, $n = 34$).

250 We also explored possible interactions between ivy stems growing on the same trunk. The basal
251 area of other stems on the same host tree was negatively related to the ivy growth rate over the last
252 five years (Pearson's $r = -0.36$, $p < 0.05$, $n = 43$) and over the last ten years ($r = -0.31$, $p < 0.05$, $n =$
253 43). To analyze this finding in greater detail, we tested whether ivy growth was related to the
254 surface available on the tree trunk for each ivy stem, calculated as the ratio between the trunk
255 circumference and the sum of ivy stems' diameters. Available space was positively correlated to the
256 growth rate both over the last five years (Pearson's $r = 0.39$, $p < 0.01$, $n = 43$) and over the last ten
257 years ($r = 0.40$, $p < 0.01$, $n = 43$) (Fig. 4).

258

259

260 **DISCUSSION**

261

262 **Ivy abundance**

263 An increase in the abundance and distribution of lianas has been observed both in tropical and in
264 temperate forests over recent decades, possibly due to the increase in atmospheric CO₂, warmer
265 temperatures, and increased forest fragmentation caused by disturbances and land use changes
266 (Allen et al. 2005; Londré and Schnitzer 2006; Van der Heijden and Phillips 2008). It is therefore
267 important to carry out quantitative surveys, and to monitor temporal variations in liana incidence in
268 different forest ecosystems (Ladwig and Meiners 2010b; Schnitzer and Bongers 2011). It is usually
269 assumed that lianas have higher incidence in tropical than in temperate ecosystems (Schnitzer and
270 Bongers 2002; Leicht-Young et al. 2010). However, the percentage of trees carrying ivy in the Siro
271 Negri alluvial forest (45 - 79%) was similar to those observed in many mature tropical and
272 subtropical forests (Putz 1984; Campanello et al. 2007; Nesheim and Økland 2007); while the
273 number of stems and basal area per hectare was lower than that generally found in tropical forests
274 (Schnitzer and Bongers 2002; Schnitzer et al. 2006; Van der Heijden and Phillips 2008; Madeira et
275 al. 2009; Gianoli et al. 2010). Studies in two temperate alluvial forests in the Rhine valley, France
276 (Schnitzler and Heuzé 2006), found 61.9 and 29.4 English ivy stems per hectare, both being much
277 lower than the numbers observed in the Siro Negri forest.

278 In addition to macro-ecological factors, stand density and tree size distribution can also influence
279 the quantity of liana (Van der Heijden and Phillips 2008; Madeira et al. 2009). Our survey was
280 carried out in four plots very close to each other, but differing in tree density and diameter
281 distribution. One of the plots (Plot 3) had a lower tree density compared to the others, but the
282 number of ivy stems and basal area were similar or slightly larger than in the other plots. Within the
283 same forest, patches with few but suitable supports can bear similar or larger amount of ivy than
284 patches with many less suitable trees.

285

286 **Host preference**

287 Lianas are structural parasites that require suitable supports to access the canopy. Tree attributes,
288 such as species morphological features, size and age, may alter liana–host interactions, influencing
289 liana colonization rates (Campanello et al. 2007; Blick and Burns 2011; Nogueira et al. 2011). A
290 few recent studies, conducted both in tropical and temperate forests, indicate that the availability of
291 suitable host trees may have more influence than climate and soil properties on vine and liana
292 distribution (Nesheim and Økland 2007; Van der Heijden and Phillips 2008; Leicht-Young et al.
293 2010). In our study, we scrutinized several tree attributes, some of which have rarely been
294 considered in previous research. The use of multiple models allowed the elimination of redundant
295 factors, and identification of the most important ones. Larger trees were more likely to host ivy than
296 smaller ones, and the largest host trees had the most ivy. A similar pattern has been observed in
297 several studies on lianas conducted in various ecosystems. However, different liana species exhibit
298 different host size preferences, depending on their climbing mechanism. Stem twiners and tendril
299 climbers better ascend small supports, and thus are more abundant on small diameter trees. On the
300 other hand, root climbers such as ivy adhere to trunks with adventitious roots rather than wrapping
301 around them, and prefer to ascend trees of larger diameters and rough bark (Putz 1984; Allen et al.
302 1997; Schnitzler and Heuzé 2006; Yuan et al. 2009; Madeira et al. 2009; Morrissey et al. 2009;
303 Leicht-Young et al. 2010; Blick and Burns 2011; Nogueira et al. 2011). It has been suggested that
304 large trees have more lianas because they are, generally, older than smaller ones, meaning more
305 colonization time for lianas (Campanello et al. 2007; Nesheim and Økland 2007; Ladwig and
306 Meiners 2010a). However, tree age is not usually measured directly. In our study, tree age of a sub-
307 set of trees (55% of the samples) was assessed by tree-ring analysis. This attribute turned out to be
308 less important than diameter (it was not significant in the GLMs that included diameter as a
309 predictor variable), indicating that tree age was of secondary importance in ivy colonization. This
310 suggests that large trees hosted more ivy than smaller ones mainly because they provided a larger
311 surface that could accommodate many stems.

312 The majority of studies analyzing liana-tree interactions have found evident species associations,
313 and some tree species seem to have a higher probability of being colonized. Trees with rougher bark
314 host more root climbers, because they provide a good surface to ascend. Moreover, crown
315 morphology also seems to affect liana-tree relationships, and trees with high stature, small leaves
316 and a light crown host more lianas, due to better light conditions (Nesheim and Økland 2007;
317 Morrissey et al. 2009). In the Siro Negri forest, *Q. robur* appeared to be preferred, and almost all
318 individuals of this species hosted ivy. However, thorough analysis revealed that ivy climbed *Q.*
319 *robur* trees because they were large and had few neighbors, whereas the effect of species *per se* was
320 negligible: when variations in size between species were excluded, different tree species were found
321 to be colonized to a similar degree by ivy. This finding, though, cannot be generalized, as the
322 species composition in the Siro Negri forest is limited to deciduous broadleaves, all characterized
323 by relatively rough bark in the adult phase: Schnitzler and Heuzè (2006) observed that ivy does in
324 fact show species preference in alluvial forests in northeastern France.

325 Using information on tree position in the stand, we analyzed the influence of neighboring trees on
326 the likelihood of a tree to carry ivy, to our knowledge an aspect never considered in previous
327 studies. Isolated trees, i.e. trees with few neighbors, were more likely to host ivy, and isolated host
328 trees had more ivy stems than host trees in crowded areas. As tree size and density are usually
329 inversely related, we checked whether the effect of neighborhood was discernible from that of tree
330 diameter. In the analyzed stand, the two parameters were slightly negatively correlated ($r = -0.24$).
331 However, the neighborhood ratio, expressed as the ratio between tree diameter and the sum of
332 neighbor's diameters, had a stronger (negative) relation with ivy descriptors than tree diameter
333 alone. The stepwise inclusion of neighborhood variables also enhanced the performance of all the
334 regression models. We concluded that neighborhood crowding directly influenced ivy colonization.
335 This is possibly because isolated tree trunks received more light than the others, making them more
336 attractive to light-demanding ascendant ivy stems. This finding provides an interesting contribution
337 to research on how forest structure affects lianas. Several authors report an increase in liana density

338 in disturbed areas and forest gaps, but the causes of this pattern have not yet received much
339 attention (Ladwig and Meiners 2010b; Gianoli et al. 2010). We observed that smaller numbers of
340 neighbors directly increased both tree likelihood of being colonized, and ivy abundance on host
341 trees. It is likely that the incidence of light-demanding root climbers increases when a disturbance
342 reduces the number of neighbors around surviving trees.

343

344 **Growth patterns**

345 Very little information exists on the longevity of lianas, and on what affects their growth patterns
346 (Brandes et al. 2011). In comparison to other liana species, however, relatively numerous
347 dendrochronological studies have been conducted on ivy, possibly because tree rings are more
348 evident than in many tropical liana species. The mean annual growth rate for ivy found in the Bosco
349 Negri (mean-ring width in the last five years equal to 1.05 ± 0.54 mm) and maximum age (69
350 years), were roughly comparable to those reported by other authors. Nola (1997) measured a mean
351 annual radial increment of 0.94 mm (± 0.34) and a maximum age of 68 years in southern Italy.
352 Garfi and Ficarrota (2003) found a mean ring width of 0.86 mm (± 0.25) and maximum age of 47
353 years in Sicily. Heuzè et al. (2009) reported a mean growth rate between 0.50 mm (± 0.42) and 2.06
354 mm (± 0.67), and maximum age of 66 years in northeastern France.

355 Growth pattern analysis can provide interesting indications on liana dynamics. Unlike ivy
356 distribution, we found that ivy growth was scarcely influenced by host tree characteristics and
357 neighborhood crowding. We did, however, find a slight but significant relationship between stem
358 growth and trunk surface available for each stem. We hypothesize that when many ivy stems rely
359 on the same tree, they compete. Positive interaction between liana stems has been reported, but this
360 was related to mechanical facilitation in the colonization of trees, as older stems provided support to
361 new ones for reaching the upper canopy (Campanello et al. 2007). We are not aware of any other
362 findings on competition between lianas, and further analyses should be conducted on other species
363 to support our finding.

364

365 **Conclusions**

366 Ivy is an important component of temperate forests but, especially outside Europe, it is often
367 regarded as a threat to other woody plants. Management of this species should be driven by better
368 knowledge of its ecology. As a structural parasite, its distribution depends strongly on the
369 availability of suitable host trees. Light-demanding climbing ivy stems ascend trees to reach better
370 light conditions. Indeed, we observed that preferred hosts were large, isolated trees that probably
371 receive more light than others. Tree species and tree age appeared weakly related to ivy distribution.
372 We conclude that the climbing form of ivy can be limited by an increase in neighborhood crowding
373 around potential host trees, i.e. by natural forest closure in the absence of disturbances. Competition
374 between ivy stems relying on the same trunk could also limit the vertical colonization of host trees.

375

376 **Acknowledgments**

377 This study was funded by the Siro Negri National Forest Reserve and by the *Ministero dell'*
378 *Ambiente e della tutela del Territorio e del Mare*. The authors thank F. Sartori, the Reserve
379 Director, L. Gianoli and M. Granata of the University of Pavia, R. Berretti, A. Bottero, F. Meloni
380 and R. Motta of the University of Turin for field assistance, providing data from previous surveys,
381 and helpful comments on this manuscript, and C. Archibald for revising English.

382

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491 **TABLES**

492

493 **Table 1** Tree stand characteristics and percentage of trees hosting ivy in the study plots

494

Density (n/ha)	Mean diameter (cm)	Basal Area (m ² /ha)	Host trees (%)
498	26.7	28.4	48
560	28.1	34.7	45
122	46.6	20.9	79
228	30.2	18.5	55
320	33.9	24.5	52

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521 **Table 2** Results of binary logistic regression to evaluate the host tree characteristics that determine
 522 the presence of ivy on a tree

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	Nagelkerke R ²	Hosmer - Lemeshow Test	Percentage Correct	Variable	Beta	Wald	p	95.0% C.I. lower	95.0% C.I. upper
Model	0.303	0.569	69.5	Diameter	0.060	15.853	<0.001	1.032	1.092
				Neighbors	-0.111	25.266	<0.001	0.857	0.934
				Species		9.582	0.088		
				Constant	-0.564	0.401	0.527		

524

525 Diameter is the diameter at breast height of the tree, neighbors is the number of trees in a circle of
 526 10 m around the tree, and species is tree species. p values < 0.05 are indicated in bold

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555 **Table 3** Results of General Linear Models to predict the number of ivy stems on host trees, the sum
 556 of their diameters, and basal area
 557

Model	Number of stems			Sum of diameters			Basal area		
	R ² Adj	Beta	p	R ² Adj	Beta	p	R ² Adj	Beta	p
Model	0.402		<0.001	0.375		<0.001	0.286		<0.001
Intercept		-0.530	0.302		-0.629	0.373		-3.451	0.018
Diameter		0.717	<0.001		0.704	<0.001		1.435	<0.001
Neighbors		-0.025	0.008		-0.030	0.021		-0.055	0.040
Quercus		-0.534	0.041		0.626	0.080		1.355	0.065
Robinia		-0.090	0.741		-0.004	0.992		0.532	0.489
Acer		-0.541	0.068		0.265	0.514		1.340	0.108
Ulmus		-0.428	0.159		-0.075	0.857		0.873	0.307
Crataegus		-0.726	0.004		0.112	0.742		0.893	0.204

558
 559 Diameter is the diameter at breast height of the tree, neighbors is the number of trees in a circle of
 560 10 m around the tree, and Quercus, Robinia, Acer, Ulmus and Crataegus are tree species. p values <
 561 0.05 are indicated in bold

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583 **FIGURE CAPTIONS**

584

585 **Fig. 1** Ivy density expressed as the number of stems per hectare ≥ 0.5 , 1 and 2.5 cm in the four
586 study plots

587

588 **Fig. 2** Ivy basal area per hectare (considering stems ≥ 0.5 cm) in the four study plots

589

590 **Fig. 3** Redundancy analysis ordination biplots. In the upper RDA (Fig. 3a), all 374 trees were
591 included, and tree age was not considered. In the lower RDA (Fig. 3b), only the 207 trees for which
592 tree age was estimated were included. Full-line arrows represent the biplot scores of tree variables:
593 TR_d = tree diameter; TR_age = tree age; NE_n = number of neighbors in a circle of 10 m around
594 the tree; NE_s_d = sum of diameters of neighbors; NE_ra = neighborhood ratio. Dotted arrows
595 represent the biplot scores of ivy descriptors: HE_n = number of ivy stems on the tree; HE_s_d =
596 sum of diameters; HE_ba = basal area; HE_d_M = diameter of the biggest stem; HE_cl = class of
597 occupancy. The dots represent tree species: Acer, Crataegus, Quercus, Robinia, Ulmus and Others

598

599 **Fig. 4** Relationship between trunk circumference available to ivy stem (i.e. the ratio between host
600 trunk circumference and sum of ivy stem diameters) and its mean ring width over the last 5 years.
601 Both axes are log-scaled. The straight line is the linear regression fitted to the data, with confidence
602 intervals (dotted lines)

Fig1

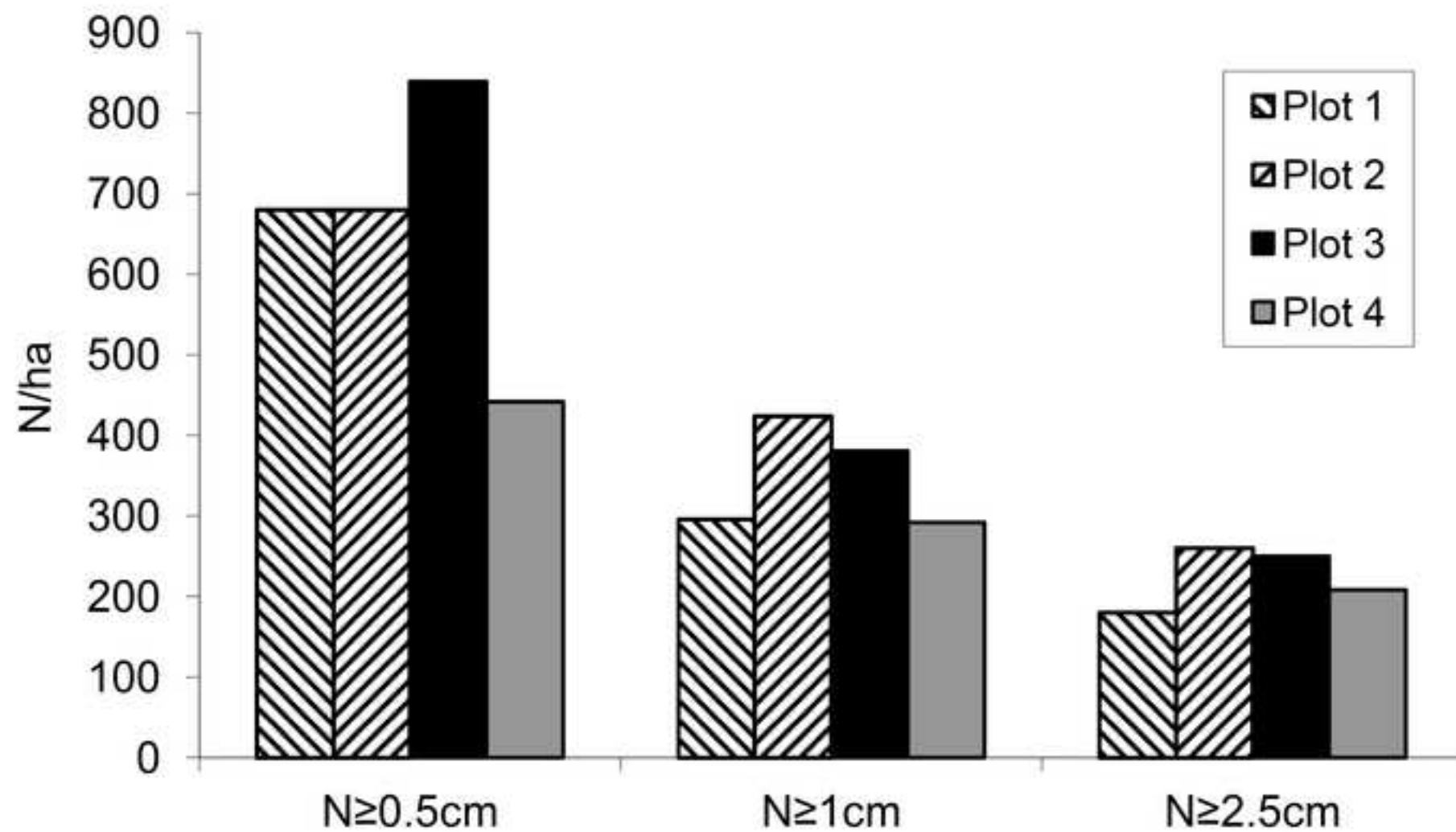
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Fig2

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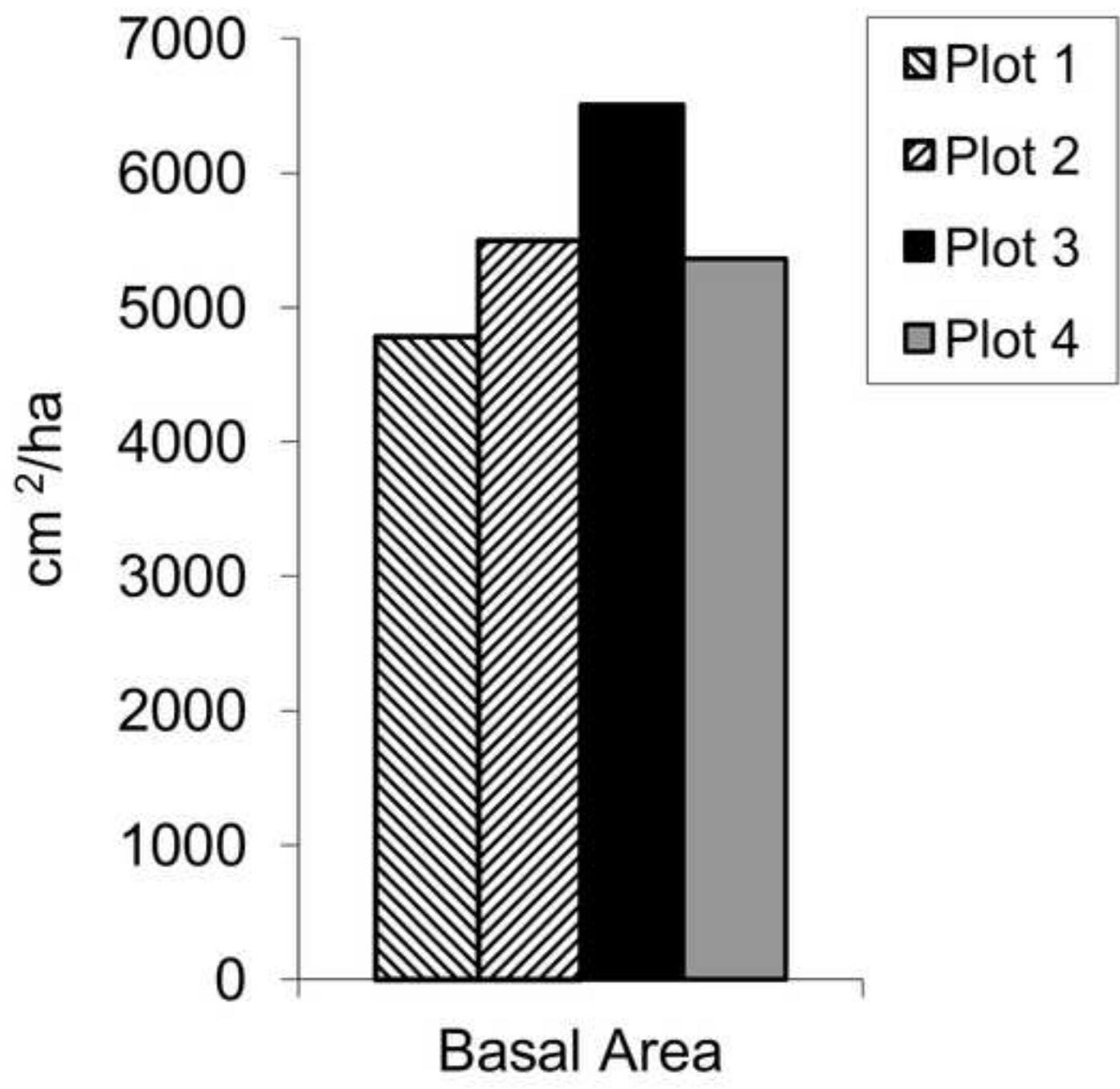


Fig3a

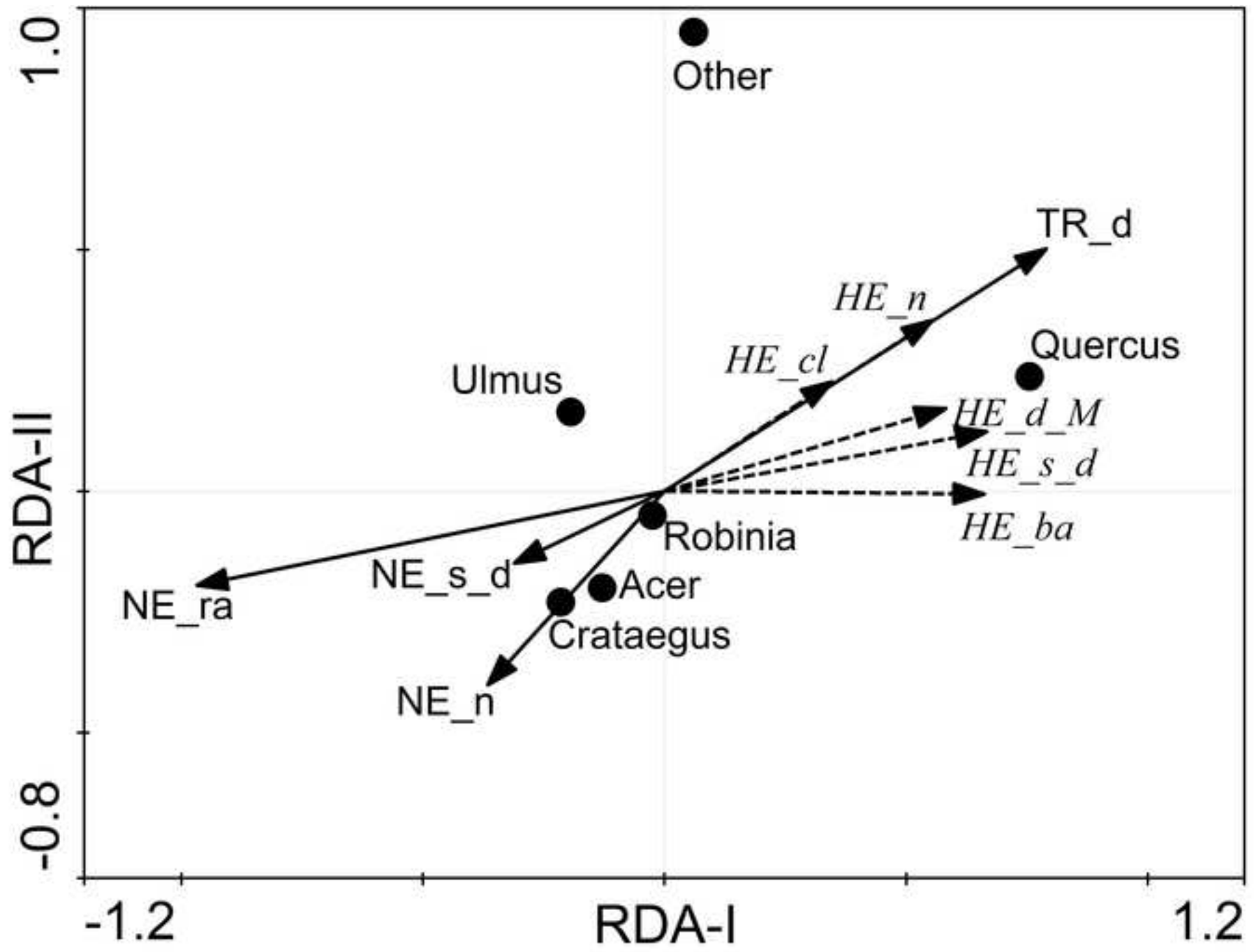
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Fig3b

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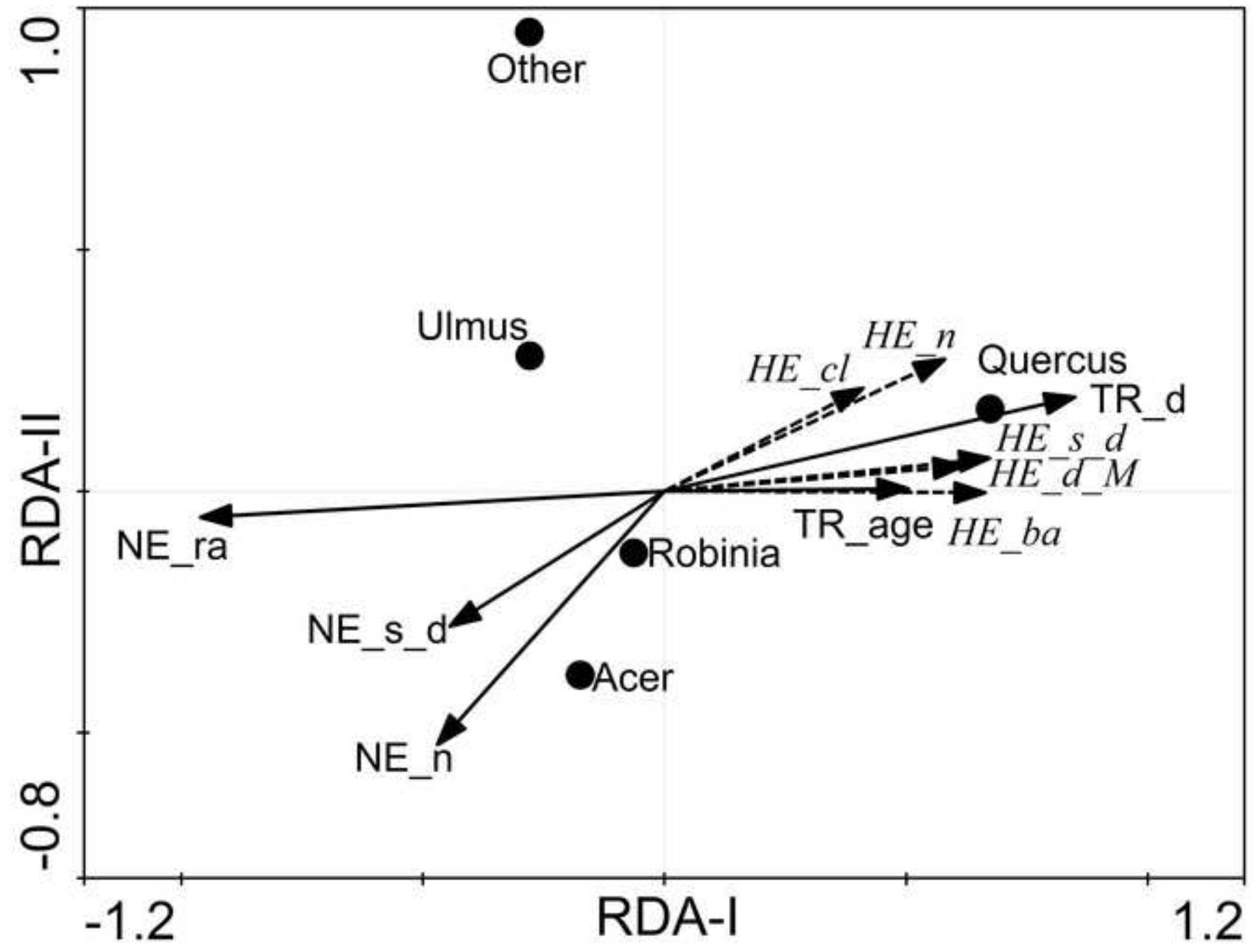


Fig4

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