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### **Threshold dynamics in plant succession after tree planting in agricultural riparian zones.**

Bourgeois, Bérenger; Vanasse, Anne; Gonzalez, Eduardo; Andersen, Roxane; Poulin, Monique

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1 **Full title**

2 Threshold dynamics in plant succession after tree planting in agricultural riparian  
3 zones

4

5 **Running title**

6 Threshold dynamics in reforested riparian zones

7

8 **Authors**

9 Bérenger Bourgeois<sup>1,2</sup>, Anne Vanasse<sup>1</sup>, Eduardo González<sup>3,4</sup>, Roxane Andersen<sup>5</sup> and  
10 Monique Poulin<sup>1,2</sup>

11

12 <sup>1</sup> Département de Phytologie, Faculté des Sciences de l'Agriculture et de l'Alimentation,  
13 Université Laval, 2425 rue de l'agriculture, Québec, Québec, G1V 0A6, Canada.

14 <sup>2</sup> Québec Centre for Biodiversity Science, Department of Biology, McGill University, Stewart  
15 Biology Building, 1205 Dr. Penfield Avenue, Montréal, Québec, H3A 1B1, Canada.

16 <sup>3</sup> Department of Biological Sciences, University of Denver, F W Olin Hall, Room 102, 2190 E  
17 Iliff Avenue, Denver, Colorado, 80208-9010, USA.

18 <sup>4</sup> EcoLab, Université Paul Sabatier, Institut National Polytechnique de Toulouse, Centre  
19 National de la Recherche Scientifique, 118 Route de Narbonne Bâtiment 4R1, 31062  
20 Toulouse Cedex 9, France.

21 <sup>5</sup> Environmental Research Institute, University of the Highlands and Islands, The North  
22 Highland College, Thurso, Scotland, United Kingdom.

23

24 Corresponding author: Département de Phytologie, Faculté des Sciences de l'Agriculture et de  
25 l'Alimentation, Université Laval, Pavillon Paul-Comtois, 2425, rue de l'Agriculture, Québec,  
26 Québec, G1V 0A6, Canada; berenger.bourgeois.1@ulaval.ca;  
27 monique.poulin@fsaa.ulaval.ca.

28

29 **Summary**

30 1. Trajectories of plant communities can be described by different models of plant  
31 succession. While a clementsian (gradual continuum model) or gleasonian approach  
32 (relay floristics model) have traditionally been used to inform restoration outcomes,  
33 alternative succession models developed recently may better represent restoration  
34 trajectories. The threshold dynamics succession model, which predicts an abrupt  
35 species turnover after an environmental threshold is crossed, has never been used in a  
36 restoration context. This model might, however, better describe shifts in plant  
37 competitive ranking and facilitation interactions during species turnover.

38 2. Fifty-three riparian zones, planted with trees 3 to 17 years prior to sampling, and 14  
39 natural riparian forests were studied in two agricultural watersheds of south-eastern  
40 Québec (Canada). The cover of vegetation strata was assessed at the site-scale, and  
41 the cover of plant species was estimated in a total of 784 1-m<sup>2</sup> plots. Canopy cover  
42 was measured stereoscopically for each plot.

43 3. As revealed by Principal Response Curves (PRC) and broken stick models,  
44 herbaceous species composition was stable during the first 12–13 years after tree  
45 planting, but then abruptly shifted. This two-step pattern in species turnover followed  
46 the increase of canopy cover after tree planting. Once canopy cover passed a threshold  
47 of *ca* 40%, plant succession started and led to the re-establishment of forest  
48 communities 17 years after planting.

49 4. Following herbaceous species turnover, the cover of ecological groups changed  
50 significantly toward covers of natural riparian forests: shade-tolerant species generally  
51 increased while light-demanding and non-native species decreased. Vegetation

52 structure was also significantly affected by tree planting: tree and shrub cover  
53 increased while monocot cover decreased.

54 5. *Synthesis and applications.* Tree planting efficiently restored herbaceous forest  
55 communities in riparian zones by inducing a species turnover mediated by light  
56 availability corresponding to threshold dynamics model in plant succession. Fostering  
57 and monitoring canopy closure in tree-planted riparian zones should improve  
58 restoration success and the design of alternative strategies. The innovative statistical  
59 approach of this study aiming to identify succession patterns and their associated  
60 theoretical models can guide restoration in any type of ecosystem around the world to  
61 bridge the gap between science and management.

62

### 63 **Key-words**

64 Agricultural landscapes, canopy cover, herbaceous communities, light availability,  
65 resilience, restoration ecology, riparian zones, succession models, vegetation recovery

66

### 67 **1. Introduction**

68 Succession models inform our understanding of ecosystem dynamics by predicting  
69 the resilience of ecosystems, their response to disturbances and the underlying  
70 assembly rules of plant communities (Young, Petersen & Clary 2005; Hobbs &  
71 Suding 2009; Alday & Marrs 2014). For degraded plant communities, succession  
72 models are helpful tools to first assess restoration trajectories, and then define  
73 achievable restoration goals or design adaptive restoration practices (Hobbs & Suding  
74 2009). Traditionally, two succession models have been used to interpret restoration  
75 outcomes: (i) gradual continuum models based on a clementsian view of plant  
76 communities predicting a deterministic linear species turnover proportional to

77 environmental changes (Clements 1916), and (ii) relay floristic models based on a  
78 gleasonian approach predicting a sequential replacement of species through autogenic  
79 facilitation and inhibition interactions (Gleason 1926; Connell & Slatyer 1977).

80 More recently, emerging theoretical frameworks have however conceptualized  
81 alternative succession models (Hobbs & Suding 2009). In particular, threshold  
82 dynamics models which predict an abrupt shift of species composition when an  
83 environmental threshold is crossed might be particularly relevant to evaluate  
84 restoration trajectories and improve or redesign restoration strategies (Bestelmeyer  
85 2006; Groffman *et al.* 2006; Suding & Hobbs 2009). In this context, time-series  
86 analyses are powerful tools that can reveal temporal patterns of species dynamics. By  
87 targeting relative species turnover against a reference system, Principal Response  
88 Curves (PRC; Van den Brink & Ter Braak 1999) are a particularly relevant approach  
89 to compare restoration strategies (Vandvik *et al.* 2005), identify the species driving  
90 community dynamics (Poulin, Andersen & Rochefort 2013) and detect alternative  
91 states (Alday & Marrs 2014). Furthermore, PRC might also have the potential to  
92 reveal the succession model involved in species turnover after restoration, but have  
93 never been used with such objective.

94 In forest restoration, the introduction of nurse species is a widely used passive  
95 strategy based on a gleasonian approach (Byers *et al.* 2006; Padilla & Pugnaire 2006;  
96 Gómez-Aparicio 2009). Nurse species are indeed assumed to modify abiotic  
97 conditions (e.g. light availability, nutrient content, etc.) and create new ecological  
98 niches suitable for the gradual spontaneous recolonization of desired species (Hobbs  
99 & Suding 2009; Paquette & Messier 2010; McClain, Holl & Wood 2011). Yet  
100 introducing a nurse species is not a guarantee that passive recolonization will occur.  
101 While planting trees in riparian forests can induce a shift in herbaceous species

102 composition after 10 to 15 years (e.g. McClain, Holl & Wood 2011; Harris *et al.*  
103 2012), the entire community usually fails to re-establish. As a result, desired  
104 recalcitrant species must be actively introduced once the canopy has developed  
105 closure (Brudvig, Mabry & Mottl 2011; McClain, Holl & Wood 2011). Given that  
106 herbaceous vegetation is a critical component of ecosystem functions and dynamics  
107 (Nilsson & Wardle 2005; Gilliam 2007), these partial restoration successes call for  
108 more research on herbaceous dynamics after tree planting. The decrease of light  
109 availability after tree planting which is a major driver for the recolonization of  
110 herbaceous species (Barbier, Gosselin & Balandier 2008; Harris *et al.* 2012), may act  
111 as a key environmental threshold for species turnover. Despite being previously  
112 described in rangelands (Friedel 1991), threshold dynamics models have never been  
113 investigated as potential models to inform succession of herbaceous species in tree-  
114 planted agricultural riparian zones, and design restoration strategies accordingly.

115 In agricultural landscapes, multiple large-scale environmental factors related to  
116 intensive land use such as habitat fragmentation and intensive use of fertilizers and  
117 pesticides can impact restoration trajectories and outcomes (Allan 2004; Tschardtke *et*  
118 *al.* 2005). Such land-use intensification could cause the low recolonization of  
119 herbaceous species and the establishment of alternative stable states through a number  
120 of processes including the impoverishment of the regional species pool (Brudvig  
121 2011), the homogenization of local abiotic conditions (Vellend *et al.* 2007), the  
122 decrease of landscape connectivity (Tschardtke *et al.* 2005) and the limitation of plant  
123 dispersal (Hermy & Verheyen 2007). In riparian systems, however, the spatial  
124 connectivity provided by water flows generally overcomes dispersal limitation, at  
125 least for hydrochorous species (Tabacchi *et al.* 1998; Nilsson *et al.* 2010). Riparian  
126 plant species can be expected to passively recolonize ecosystems through water

127 dispersal once their ecological niches have been restored (*Field of Dreams*  
128 *Hypothesis*, “if you build it, they will come”; Palmer, Ambrose & Poff 1997).  
129 However, in degraded riparian zones, hydrological connectivity also contributes to the  
130 high prevalence of biological invasions (Richardson *et al.* 2007) which are among the  
131 primary drivers of the establishment of non-desired alternative stable states (Suding,  
132 Gross & Houseman 2004; Didham *et al.* 2005). Identifying potential ecological  
133 thresholds driving species turnover and possibly leading to alternative states can not  
134 only inform theories of plant succession, but also the restoration of forested riparian  
135 zones in intensively managed agricultural landscapes.

136 Therefore, the goal of this study was to assess the successional trajectory followed by  
137 herbaceous communities after tree planting in riparian zones of agricultural  
138 landscapes. We propose to use for the first time a combination of statistical  
139 approaches including PRC to provide a mechanistic interpretation of riparian  
140 community assemblages over time. We predicted that tree planting would initiate a  
141 plant succession leading to the re-establishment of forest herbs after the crossing of an  
142 ecological threshold in canopy cover. Besides species composition, we evaluated  
143 whether tree planting re-established an herbaceous vegetation characteristic of natural  
144 riparian forests in terms of vegetation structure and herbaceous ecological groups.

145

## 146 **2. Materials and methods**

### 147 *2.1. Study area*

148 This study was conducted in two agricultural watersheds of south-eastern Québec  
149 (Canada; Appendix S1 in Supporting Information). The Boyer watershed (46°41' N  
150 70°55' W) is a 216-km<sup>2</sup> area mainly devoted to agriculture (66% of land use), with  
151 scattered forest fragments (24% of land use). Between 1948 and 1992, some 73% of

152 the 251 km of rivers flowing through the area were channelized to increase soil  
153 drainage and improve cultivation of annual crops (e.g. wheat, corn and soybean). On  
154 this watershed, annual crops represent 26% of agricultural land use (OBV Côte-du-  
155 Sud/GIRB 2011). The Bélair watershed (46°26' N 70°56' W) is a 43-km<sup>2</sup> area with a  
156 high cover of forests (66% of land use). Agricultural production covers 14 km<sup>2</sup> (or  
157 33%) of this watershed, of which 18% is devoted to annual crops (MAPAQ  
158 *unpublished data*). Besides channelization, signs of riverbank erosion were also  
159 identified during field work along the studied river reaches. To mitigate  
160 environmental degradations caused by agricultural intensification and improve the  
161 provision of ecosystem services, agricultural practices were banned on a buffer of at  
162 least 3-m wide along streams (Gouvernement du Québec 1987). From 1995 to 2009,  
163 extensive tree planting projects in riparian zones were conducted by local  
164 stakeholders of the two studied watersheds. The primary objective of tree planting  
165 was to increase water filtration and reduce soil erosion rather than to recover riparian  
166 trees such as natives *Salix* or *Populus* spp. Consequently, the most frequently planted  
167 tree species corresponded to *Fraxinus pennsylvanica* Marsh., *Acer saccharum* Marsh.,  
168 *Picea glauca* (Moench) Voss, *Larix laricina* (Du Roi) K. Koch, *Quercus rubra* L. and  
169 *Quercus macrocarpa* Michx., all natives in the study area. Planting techniques were  
170 generally uniform over time and consisted in the planting of 30-cm tall trees in bare  
171 soil every 3–5 m along a single row on the flat edges of agricultural fields (i.e. on  
172 average 5m away from the field margins) without replacement of dead trees in the  
173 successive years.

174

175 *2.2. Sampling design*



176 During the summer of 2012, 53 riparian zones representing a chronosequence of 3 to  
177 17 years after tree planting were sampled along relatively uniform rivers (in terms of  
178 width and flow) within the two watersheds studied (Appendix S1). To ensure site  
179 representativeness and uniformity in local environmental and agricultural conditions,  
180 four conditions had to be met by a tree-planted riparian zone in order to be sampled,  
181 i.e. (i) measure at least 40 m long, (ii) have been planted with trees within a single  
182 year, (iii) be adjacent to an agricultural field with uniform crops, (iv) have a uniform  
183 vegetation structure. As a space-for-time substitution was used to assess the temporal  
184 dynamics of riparian plant communities after tree planting, sites were also selected to  
185 obtain a complete sampling of the 3–17 year chronosequence uniformly distributed  
186 over the study area. In addition to these 53 tree-planted riparian zones, 14 mature  
187 natural riparian forests were also sampled as reference ecosystems. These natural  
188 forests corresponded to the last remnants of natural riparian habitats occurring  
189 throughout the study area and were generally dominated by *Fraxinus pennsylvanica*,  
190 *Acer saccharum* and *Quercus* spp., which were also among the most frequently  
191 planted tree species.

192

### 193 2.3. Botanical surveys

194 Vegetation structure was assessed at each site by recording the cover of tree (> 5 m  
195 high), shrub (1–5 m), dicot herbs, monocot herbs (hereafter Dicots and Monocots)  
196 and pteridophyte strata using the Braun-Blanquet index (0.5: < 1% cover; 1: 1–5%  
197 cover; 2: 5–25% cover; 3: 25–50% cover; 4: 50–75%; 5: > 75% cover). Two surveys  
198 of vegetation structure were conducted along the entire length of each sampling site,  
199 the first along the flat edge of the agricultural field where trees were planted, the  
200 second along the spontaneous (unplanted) plant communities of the sloped riverbanks.

201 Herbaceous composition was sampled by visual estimation of species cover (%) in 1-  
202 m<sup>2</sup> plots along equidistant transects perpendicular to the river from the field edge to  
203 the riverbank. Canopy cover (%) over plots was estimated based on stereoscopic  
204 measurements taken at a height of 1-m height above ground level (24 MP DSLR  
205 System and WinSCANOPY software, Regent Instruments Inc., Québec, Canada). To  
206 obtain an accurate botanical survey accounting for the intra-site variability of plant  
207 communities, the number of transects at each site was proportional to the site length  
208 and the number of plots along each transect proportional to the transect length. More  
209 precisely, plant communities were sampled along two (sites shorter than 100 m) to  
210 five transects (sites longer than 200 m; max length: 1150 m) per site, into two 1-m<sup>2</sup>  
211 plots (transect shorter than 5 m; one plot on the field edge, one on the riverbank) to  
212 six equidistant plots (transect longer than 40 m; the number of plots on the field edge  
213 and on the riverbank depended on slope break) along each transect (Appendix S2).  
214 Since a preliminary principal component analysis showed a different species  
215 composition for field edges and riverbank plots (Appendix S3), all subsequent  
216 analyses were conducted separately for these two communities. Consequently, a  
217 community-weighted mean of species cover from all plots was calculated separately  
218 for the field edge and the riverbank of each site. Two observations of plant species  
219 abundance were thus obtained per site.

220 Herbaceous plant species inventoried were then classified into six ecological groups  
221 related to their light requirements (shade-tolerant vs. light-demanding species), their  
222 origin (native vs. non-native) and their wetland status (wetland obligate vs. wetland  
223 facultative) based respectively on local floras (Marie-Victorin, Brouillet & Goulet  
224 1995), the data base of Vascular Plants of Canada (Brouillet *et al.* 2010) and  
225 governmental classification (MDDEP 2012). These three types of species grouping

226 were selected considering their potential response to restoration, i.e. (i) canopy  
227 closure after tree planting is likely to increase the shade levels experienced by  
228 herbaceous species, (ii) colonization by native species is a desirable outcome of a  
229 restoration project, and (iii) wetland obligates and facultatives are characteristic  
230 species of riparian forests that might benefit from restoration. Among the 203  
231 herbaceous species inventoried in the 784 1-m<sup>2</sup> plots within the 67 sampled riparian  
232 zones, 26% were shade-tolerant and 74% light-demanding, 61% native and 39% non-  
233 native, 23% wetland obligate and 15% wetland facultative (62% were non-wetland  
234 species; Appendix S4). The total cover of these six groups was then calculated for the  
235 field edge and riverbank of each site as the sum of covers of the corresponding  
236 species.

237

#### 238 *2.4. Statistical analysis*

239 Plant succession in herbaceous riparian communities after tree planting was evaluated  
240 with a PRC, using natural riparian forests as a comparison benchmark. Site scores  
241 along the PRC axis were then used in a broken stick regression against the time  
242 elapsed since tree planting to identify threshold in species turnover (Toms &  
243 Lesperance 2003). Compositional differences between tree-planted riparian zones and  
244 natural riparian forests were assessed based on a linear mixed model with site scores  
245 along the PRC axis as response variable, treatment (tree-planted riparian zones vs.  
246 natural riparian forests) and the time the elapsed since tree planting (in years) as  
247 explanatory variables and site as random factor; a Bonferroni correction was applied  
248 to assess the significance of each contrast, here  $\alpha = 0.0056$  (see also Alday & Marrs  
249 2014). Indicator species of natural riparian forests were also identified using IndVal  
250 analysis (Dufrêne & Legendre 1997) to assess whether these species were positively

251 correlated with the PRC axis and thus re-established after tree planting. For each  
252 ecological group (shade-tolerant, light-demanding, native, non-native, wetland  
253 obligate and wetland facultative), a mean score along the PRC axis was finally  
254 calculated from the scores of its associated species, to evaluate ecological  
255 mechanisms likely to drive species turnover after tree planting.

256 The existence of thresholds in the temporal dynamic of canopy cover with the time  
257 elapsed since tree planting was assessed using a binary segmentation which enables  
258 the detection of multiple thresholds (Killick, Fearnhead & Eckley 2012), followed by  
259 an ANOVA and Tukey post-hoc tests to evaluate the significance of the detected  
260 thresholds. A linear regression was then performed between site scores along PRC  
261 axis and canopy cover to quantify the strength of the relationship between canopy  
262 cover and species turnover, and thereby the driving role of light availability in plant  
263 succession.

264 The temporal evolution of cover after tree planting was assessed using a generalized  
265 linear model (GLM) followed by Tukey post-hoc tests for each of the six ecological  
266 groups (abundances expressed in %; GLM with a Gaussian distribution) and each of  
267 the five vegetation strata (abundances expressed with Braun-Blanquet indices; GLM  
268 with a Poisson distribution). We compared mean abundances for these groups  
269 between young plantations (3–12 years), old plantations (14–17 years) and natural  
270 riparian forests to verify if the threshold detected in species turnover was  
271 accompanied by changes in herbaceous ecological groups and vegetation structure.

272 All analyses were conducted in R version 3.1.0 (R Core Team 2014) using packages  
273 *bentcableAR* (Chiu *et al.* 2015), *changeoint* (Killick & Eckley 2014), *indicpecies*  
274 (De Caceres & Legendre 2009), and *vegan* (Oksanen *et al.* 2013).

275

## 276 3. Results

### 277 3.1. Dynamics of herbaceous communities

278 Plant succession after tree planting followed a two-step pattern in both field edge and  
279 riverbank communities where abrupt changes in species composition started 12 years  
280 ( $R^2_{broken\ stick} = 92.97\%$ ) and 13 years after tree planting ( $R^2_{broken\ stick} = 88.08\%$ ),  
281 respectively (Fig. 1, left). Prior to these thresholds, the composition of herbaceous  
282 riparian communities remained relatively stable and distinct from the herbaceous  
283 composition of natural riparian forests (Fig. 1, left). Once these thresholds were  
284 passed, a rapid turnover of herbaceous species occurred, leading to the re-  
285 establishment of forest plant communities at the end of the chronosequence. While  
286 noticeable species turnover began 12 to 13 years after tree planting, at least 17 years  
287 were necessary to recover herbaceous plant communities similar to those of natural  
288 riparian forests both at field edges ( $t = -2.85$ ;  $P = 0.0061$ ) and along riverbanks ( $t = -$   
289  $2.69$ ;  $P = 0.0094$ ; Fig. 1). Moreover, all the indicator species of natural riparian  
290 forests were characterized by high positive scores along the PRC axis (Fig. 1, middle).  
291 The observed species turnover more precisely corresponded to the replacement of  
292 weeds, graminoids and ruderal species, like *Bromus inermis* L., *Phalaris arundinacea*  
293 L., *Equisetum arvense* L., *Artemisia vulgaris* L., and *Solidago canadensis* L. by ferns  
294 and forest herbs, such as *Dryopteris carthusiana* (Vill.) H.P. Fuchs, *Athyrium filix-*  
295 *femina* (L.) Roth, *Trilium erectum* L. and *Rubus pubescens* Raf., as shown by species  
296 scores along the PRC axis (Fig. 1, middle). During this turnover, shade-tolerant  
297 species associated with natural riparian forests increased at the expense of light-  
298 demanding species, while non-native species decreased but were replaced by native  
299 species characteristic of riparian natural forests only in field edge community (Fig. 1,  
300 right). Wetland obligate and facultative species associated with natural riparian forests

301 contributed less to this successional pattern, with only a slight increase of obligate  
302 species in field edge communities over time.

303

304

305

### 306 *3.2. Dynamics of canopy cover*

307 The increase of mean canopy cover over time followed three-step dynamics structured  
308 around two thresholds both in field edges and along riverbanks ( $R^2_{\text{binary segmentation}} =$   
309 83.68% and 82.89%, respectively; Fig. 2). Six years after tree planting, mean canopy  
310 cover increased from 24% to 36% in field edges and from 23% to 31% along  
311 riverbanks, and then reached 59% and 64% respectively after a second more  
312 pronounced threshold after 12 years (Fig. 2). Among these two thresholds detected in  
313 mean canopy cover, only the second one corresponded to a significant increase in  
314 canopy cover measured at each site both at field edges ( $F = 35.80$ ;  $P < 0.0001$ ) and  
315 along riverbanks ( $F = 44.26$ ;  $P < 0.0001$ ; Fig. 2). Canopy cover thus followed a  
316 temporal pattern similar to that of species turnover, i.e. a fairly stable canopy cover of  
317 ca. 20–40% during the first 12 years after tree planting (with a slight decline in the 6  
318 first years), and then an abrupt increase to ca. 60% of canopy cover. This similar  
319 dynamic was further evidenced by a strong positive relationship between mean  
320 canopy cover and site scores along the PRC axis both at field edges ( $F = 19.59$ ;  $P =$   
321 0.0031;  $R^2 = 69.91\%$ ) and along riverbanks ( $F = 20.83$ ;  $P = 0.0026$ ;  $R^2 = 71.25\%$ ; Fig.  
322 3).

323

### 324 *3.3. Dynamics of herbaceous ecological groups*

325 The total cover of ecological groups was strongly influenced by the threshold detected  
326 in species turnover 12 to 13 years after tree planting (Table 1; Fig. 4). After this  
327 threshold, the cover of light-demanding and non-native species decreased but  
328 remained higher than in natural riparian forests both at field edges and along  
329 riverbanks, while the cover of shade-tolerant species increased to reach cover levels  
330 similar to those observed in natural riparian forests at field edges (Table 1; Fig. 4).  
331 The cover of native species peaked in old plantations of field edges while for  
332 riverbanks, it remained higher in young and old plantations than in natural riparian  
333 forests. The total cover of shade-tolerant species of around 20% along riverbanks of  
334 young plantations was mainly due to generalist species able to grow under shade,  
335 notably *Agrimonia striata* Michx, *Fragaria virginiana* Duchesne, *Onoclea sensibilis*  
336 L. and *Solidago rugosa* Mill., but not associated with natural riparian forests (Fig. 1).  
337 Wetland obligate and facultative species were sparsely affected by species turnover,  
338 except for a slight decrease of wetland obligates along riverbanks.

339

### 340 3.3. Dynamics of vegetation structure

341 Once the 12–13 year threshold was passed, tree and shrub cover increased, whereas  
342 monocot cover decreased both at field edges and along riverbanks (Table 2; Fig. 5).  
343 However, in old plantations, a cover typical of natural riparian forest was only  
344 reached for trees at field edges, and for shrubs and monocots along riverbanks (Fig.  
345 5). For dicots and pteridophytes, cover remained similar over time and between tree-  
346 planted riparian zones and natural riparian forests in both field edge and riverbank  
347 communities (Fig. 5).

348

## 349 4. Discussion

350 Plant succession of tree-planted degraded ecosystems including riparian forests has  
351 generally been framed in relay floristics models (Hobbs & Suding 2009). These  
352 autogenic succession models postulate that sequential waves of species succeed one  
353 another in a linear fashion during plant succession owing to facilitation and inhibition  
354 interactions between species (Clements 1916; Connell & Slatyer 1977). However, the  
355 species turnover observed in this study suggests that an alternative model – threshold  
356 dynamics – better explains succession in tree-planted agricultural riparian zones.  
357 Herbaceous species turnover indeed followed a two-step pattern structured around an  
358 ecological threshold occurring 12 to 13 years after tree planting. Once past this  
359 threshold, species turnover started, and the herbaceous composition of riparian  
360 communities, previously stable, shifted abruptly to a species assemblage characteristic  
361 of natural riparian forests 17 years after plantation. In addition to inducing the  
362 recolonization of riparian forest species, tree planting led to the re-establishment of a  
363 vegetation structure and an abundance of ecological groups closer or similar to natural  
364 riparian forests after crossing the threshold observed in species turnover.

365 This first evidence of a threshold dynamic in agricultural riparian zones after tree  
366 planting sheds new light on the resilience capacity of riparian plant communities. In  
367 this study, no alternative stable state was indeed identified in riparian plant  
368 communities after tree planting. Despite high cover of non-natives in young  
369 plantations, these species which were generally introduced during the European  
370 settlement for agricultural purposes, did not aggressively invade plant communities,  
371 nor drove plant succession to novel assemblages. Previous findings of long-term  
372 experiments have also demonstrated a similar role of natives and non-natives in plant  
373 succession (Meiners 2007) where the trajectory rather depends on the chronological  
374 order of species arrival rather than on their origin (Yurkonis, Meiners & Wachholder



375 2005). Furthermore, the ecological impacts of agricultural activities such as dispersal  
376 limitation (related to habitat fragmentation) and modified abiotic conditions  
377 (especially increased nutrient availability due to fertilization) did not push riparian  
378 communities into alternative states, as previously observed (Cramer *et al.* 2008).

379 Tree planting appears sufficient to re-establish plant communities characteristic of  
380 natural riparian forests (which fail to recover in the absence of tree planting;  
381 D'Amour *et al. unpublished data*). Riparian zones can thus tolerate high degradation  
382 due to agricultural activities contrary to upland forest plantations, where soil  
383 compaction and low organic matter content have often been found to be critical  
384 impediments to the recovery of herbaceous diversity (Flinn & Vellend 2005; Hermy  
385 & Verheyen 2007). This high resilience of riparian plant communities might be  
386 related to regular soil re-organization caused by hydrological disturbance (González *et*  
387 *al.* 2014) and to constant inputs of propagules from the river (Tabacchi *et al.* 1998;  
388 Nilsson *et al.* 2010) that have mitigated the environmental degradation associated  
389 with agricultural land use. However, this resilience is only expressed after a critical  
390 environmental threshold has been crossed, suggesting the idea of a nonlinearity  
391 between resilience capacity and environmental conditions.

392 The synchrony of canopy closure and herbaceous plant succession as well as the  
393 replacement of shade-tolerant by light-demanding species after tree planting clearly  
394 identifies light availability as the main factor limiting the recovery of plant  
395 communities in agricultural riparian zones, with an ecological threshold in canopy  
396 cover above *ca* 40%. Similar changes attributable to light availability have previously  
397 been observed in boreal, temperate and Mediterranean forests (Gómez-Aparicio *et al.*  
398 2004; Barbier, Gosselin & Balandier 2008; Cole & Weltzin 2008; Jules, Sawyer &  
399 Jules 2008). Canopy closure also resulted in increased native species cover in

400 Australian riparian zones four years after tree planting (Cole & Weltzin 2008; Harris  
401 *et al.* 2012) and led to enrichment communities 10 years after planting in hybrid  
402 poplar plantations on abandoned fields (Boothroyd-Roberts, Gagnon & Truax 2013).  
403 Besides decreasing light availability, trees have been shown to influence herbaceous  
404 communities by modifying numerous other abiotic factors such as soil moisture, soil  
405 nutrients, microbial activities or microclimate (Barbier, Gosselin & Balandier 2008).  
406 In the context of ecological restoration, PRC has been proven to be a powerful  
407 statistical tool to identify restoration success (Vandvik *et al.* 2005), alternative stable  
408 states (Alday & Marrs 2014) and species involved in plant succession (Poulin,  
409 Andersen & Rochefort 2013). Our study identified an additional advantage of PRC,  
410 for identification of the succession model that best represents species turnover after  
411 restoration. In an innovative adaptation, species scores along the PRC axis were  
412 averaged for meaningful ecological groups, to bring further mechanistic insights into  
413 successional patterns. Such an understanding can be taken a step further when  
414 environmental variables are monitored simultaneously with plant communities. By  
415 comparing the temporal dynamics of environmental variables with species turnover, it  
416 is possible to easily discriminate the primary drivers of plant succession, as shown  
417 here for light availability. Restoration researchers and practitioners are thus  
418 encouraged to collect both species and environmental data in restored and reference  
419 habitats over time, in order to perform time-series analyses.

420 While hydro-geomorphological manipulations aiming at re-establishing the natural  
421 flow regime are considered the most efficient restoration method for recovering the  
422 ecological integrity of riparian zones (Poff *et al.* 1997; Rood *et al.* 2005), acceptance  
423 and implementation of this approach is limited by the legacies of human  
424 modifications on rivers and by the socio-economic context, especially in agricultural

425 landscapes of high economic value (Hughes & Rood 2003). In such a context – tree  
426 planting – the second most frequent restoration strategy of riparian vegetation  
427 reported in peer-reviewed literature (González *et al.* 2015), can be efficient to achieve  
428 restoration goals that maximize certain ecosystem services. For example, tree planting  
429 has been shown to influence plant succession in other types of riparian zones such as  
430 *Salicaceae*-dominated forests (e.g. Lennox *et al.* 2011) and swamps (e.g. McLane *et*  
431 *al.* 2012).

432 Successional trajectories remain difficult to interpret and can be misleading if the  
433 succession model is unknown, especially when a lengthy time delay occurs between  
434 restoration and species turnover. The identification of threshold dynamics and  
435 environmental driver(s) allows defining effective restoration approaches focused on  
436 pushing a system over environmental threshold(s). In agricultural riparian zones,  
437 planting fast-growing tree species to form a dense canopy appears an efficient  
438 restoration strategy to rapidly decrease light availability and thereby accelerate the  
439 passive re-establishment of herbaceous forest communities. Furthermore, active  
440 reintroduction of desired species should only be considered if plant composition  
441 remains stable after the threshold in light availability has been crossed, as dispersal  
442 limitation may occur. Since succession models inform our understanding of species  
443 turnover and underlying environmental drivers, their identification should improve  
444 restoration approaches.

445

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456

#### 457 **Data accessibility**

458 Plant community and environmental data can be found at

459 <http://dx.doi.org/10.5061/dryad.b46k4>

460

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630

### 631 **Supporting Information**

632 Additional Supporting Information may be found in the online version of this article:

633

634 Appendix S1. Location of the sampled riparian zones.

635 Appendix S2. Sampling design of riparian communities.

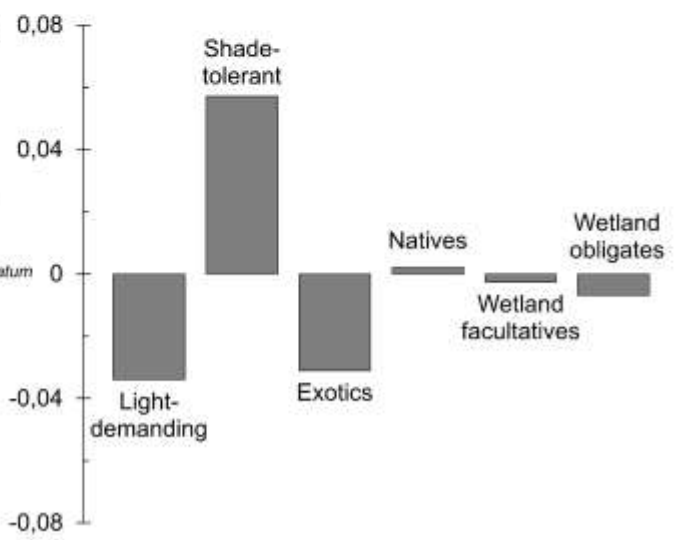
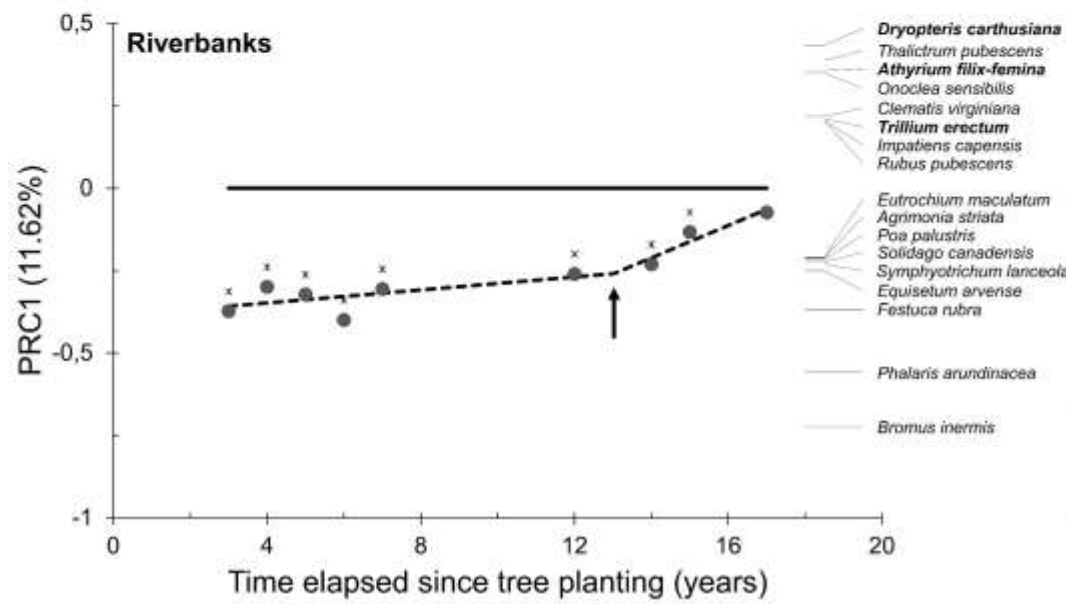
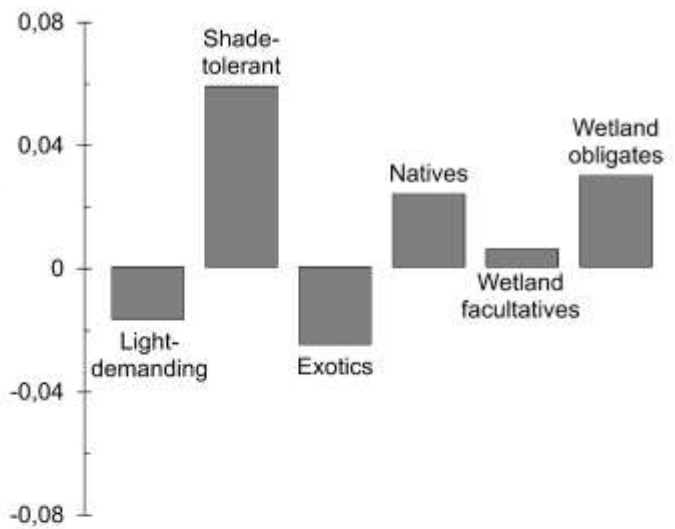
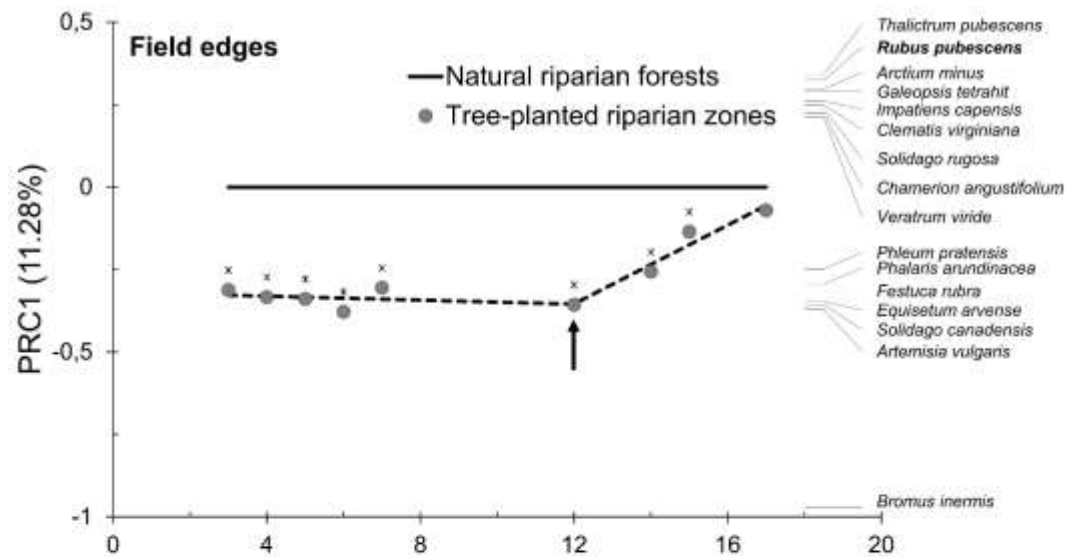
636 Appendix S3. Species-based PCA of riparian communities.

637 Appendix S4. List of the species inventoried.

638

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640



642 Fig. 1. Compositional dynamics of herbaceous riparian communities with the time elapsed  
643 since tree planting in comparison to natural riparian forests, obtained by Principal Response  
644 Curves (PRC: left side; only species with a score along axis 1 higher than  $|0.2|$  are  
645 represented; asterisks represent significant differences in species composition between tree-  
646 planted riparian zones and natural riparian forests), broken stick regression on site scores  
647 along the PRC axis against the time elapsed since tree planting (arrows indicate thresholds in  
648 species turnover) and scores of ecological groups along the PRC axis (i.e. mean score of  
649 species belonging to each group; right side). Indicator species of natural riparian forests are  
650 indicated in bold, i.e. ***Rubus pubescens*** ( $IndVal = 0.58$ ;  $P = 0.0650$ ), ***Dryopteris carthusiana***  
651 ( $IndVal = 0.65$ ;  $P = 0.0150$ ), ***Trilium erectum*** ( $IndVal = 0.60$ ;  $P = 0.0300$ ) and ***Athyrium filix-***  
652 ***femina*** ( $IndVal = 0.60$ ;  $P = 0.0450$ ).

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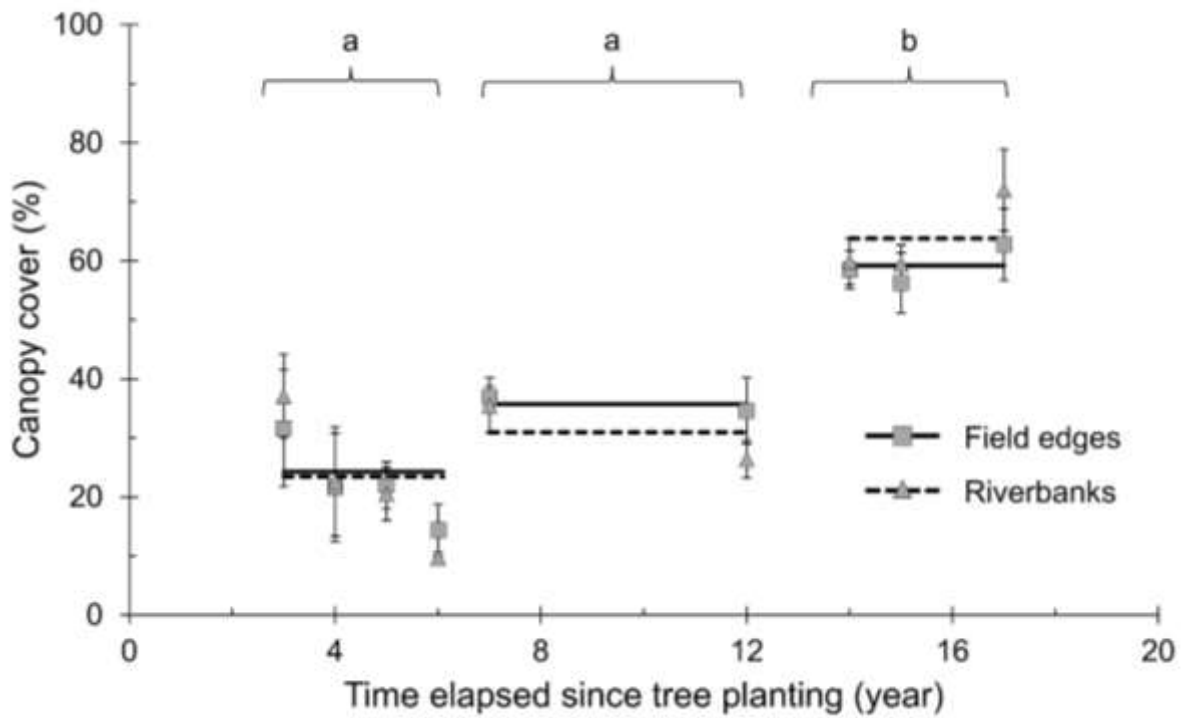
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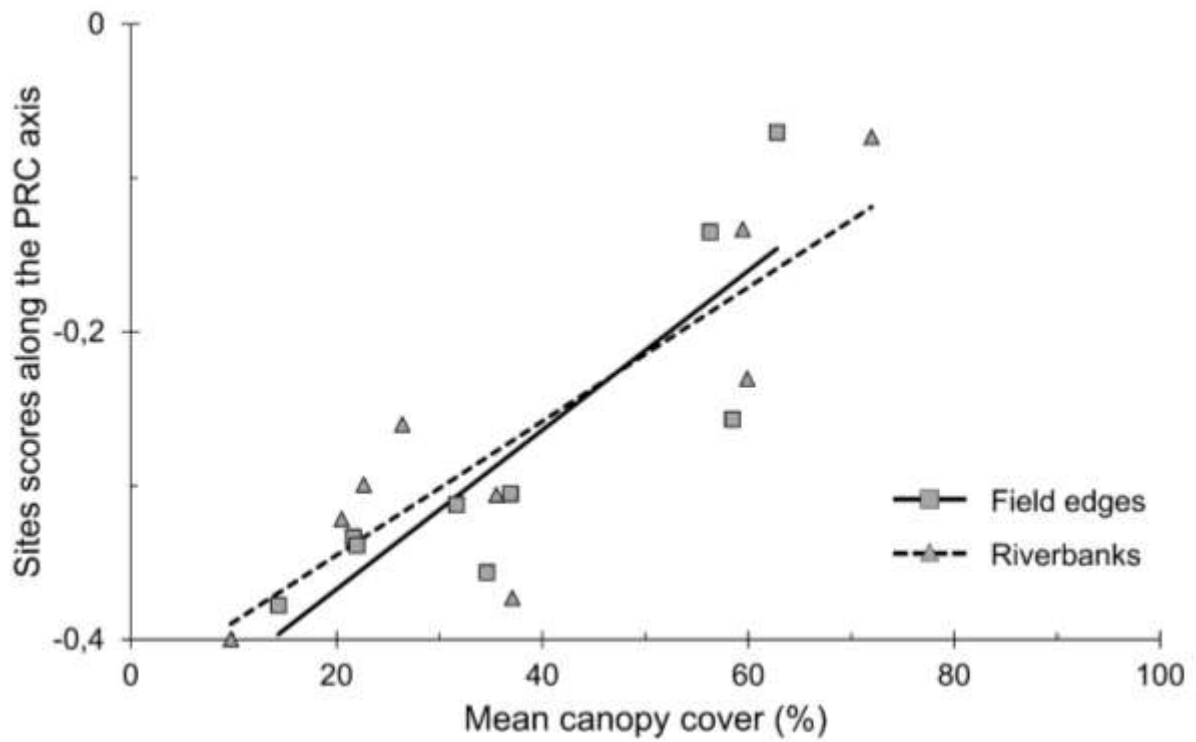


659

660 Fig. 2. Thresholds in the temporal dynamics of canopy cover (mean  $\pm$  SE) in riparian zones  
 661 with the time elapsed since tree planting, obtained by binary segmentation (lines represent  
 662 thresholds in mean canopy cover; letters correspond to significant between-threshold  
 663 differences in canopy cover measured at each site, obtained by ANOVA and Tukey post-hoc  
 664 tests). Canopy cover was calculated by stereoscopic measurements taken at a height of 1 m  
 665 above each plant inventory plot.

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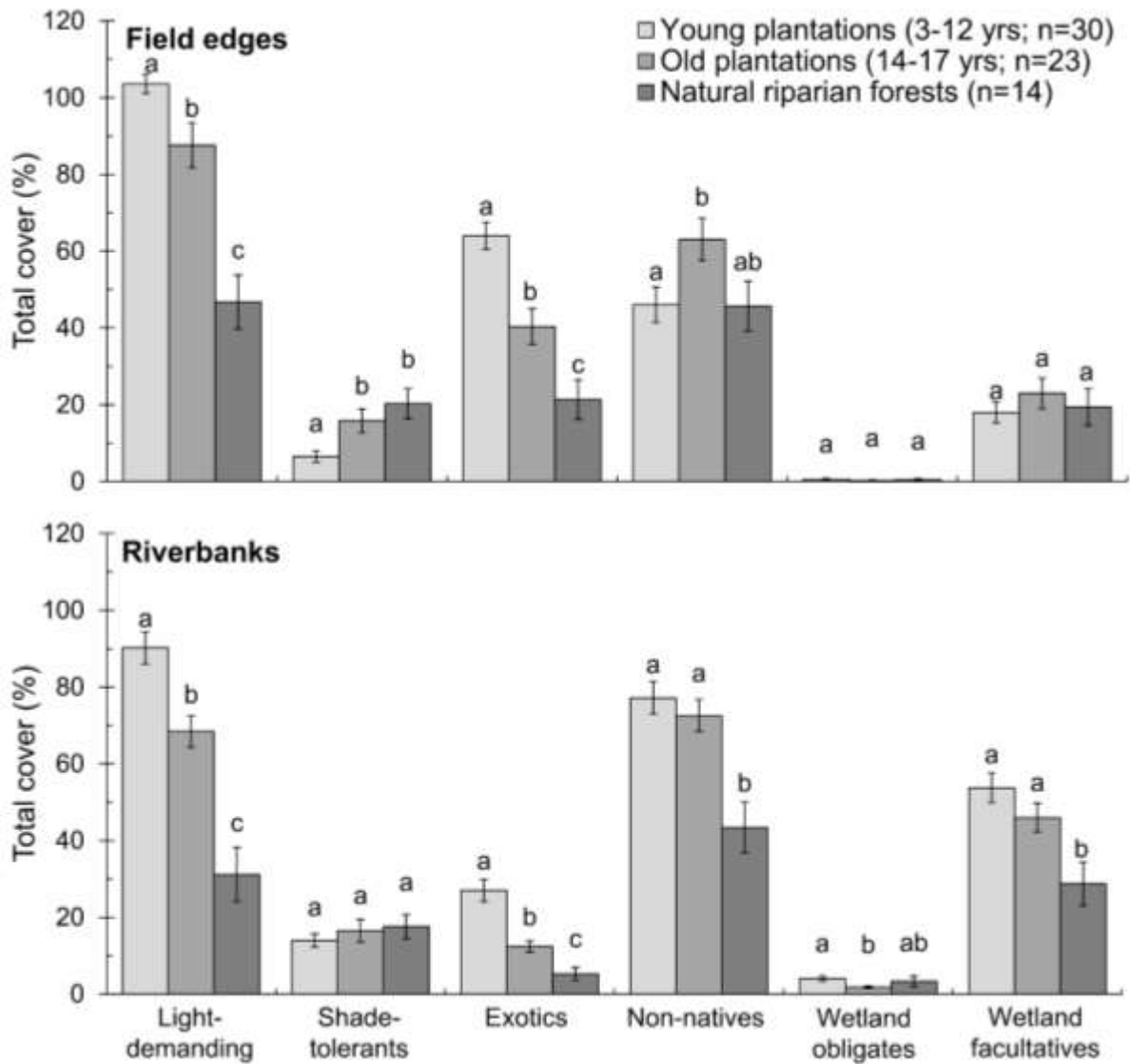


668

669 Fig. 3. Relationship between sites scores along the Principal Response Curves (PRC) axis  
 670 (see Fig. 1) and mean canopy cover, obtained by linear regression.

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672



673

674 Fig. 4. Total cover of herbaceous ecological groups (mean  $\pm$  SE) in young plantations (i.e.  
 675 observations dated before threshold in species turnover; see Fig. 1), old plantations (i.e. after  
 676 threshold) and natural riparian forests (letters correspond to significant differences obtained  
 677 by Tukey post-hoc tests).

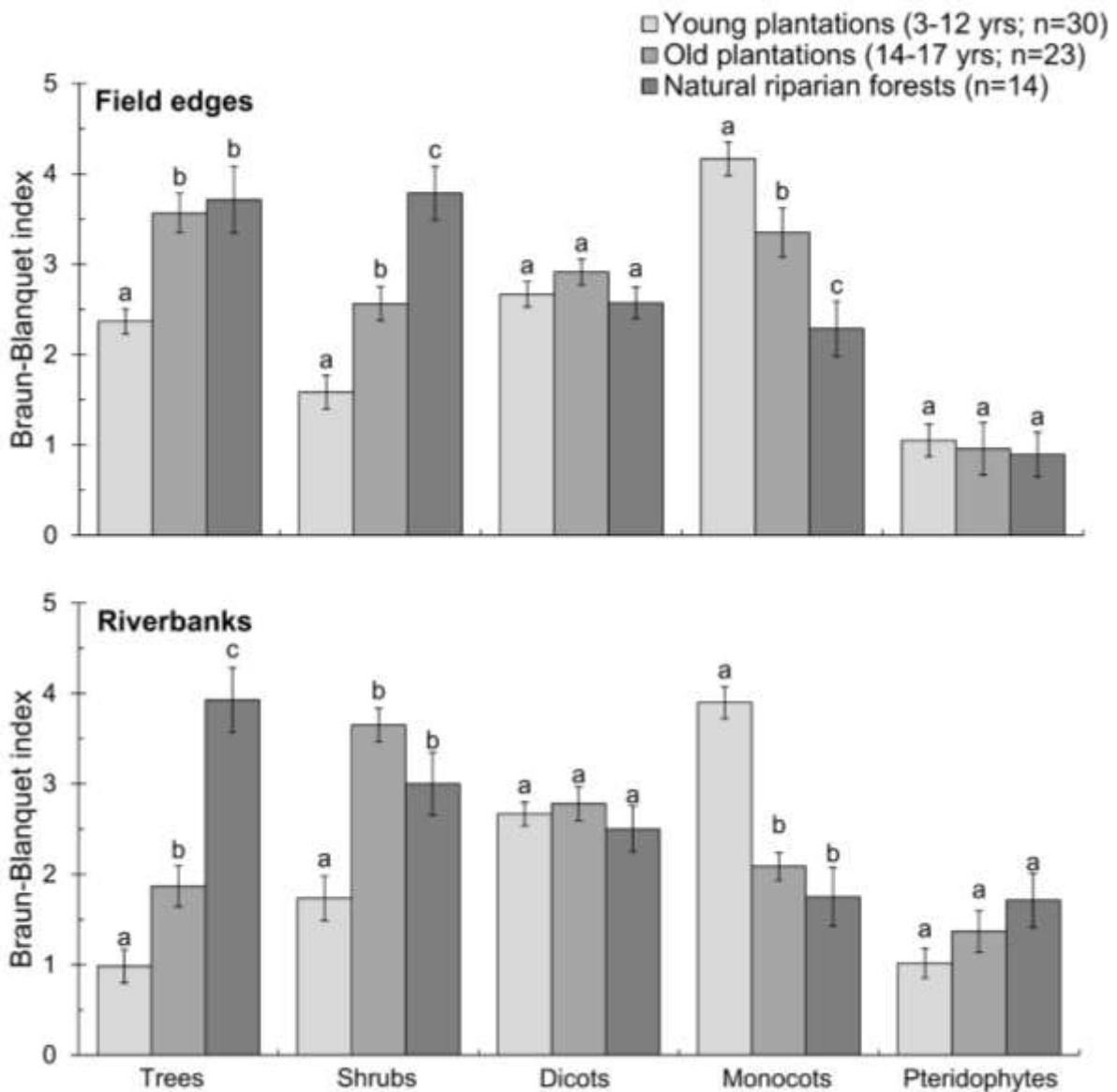
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684 Fig. 5. Cover of vegetation strata (mean  $\pm$  SE) in young plantations (i.e. observations dated  
 685 before threshold in species turnover; see Fig. 1), old plantations (i.e. after threshold) and  
 686 natural riparian forests (letters correspond to significant differences obtained by Tukey post-  
 687 hoc tests) based on Braun-Blanquet indices (0.5: < 1% cover; 1: 1–5% cover; 2: 5–25%  
 688 cover; 3: 25–50% cover; 4: 50–75%; 5: > 75% cover).

689

690

691 Table 1. Differences in the total cover of herbaceous ecological groups between young  
 692 plantations (i.e. observations dated before threshold in species turnover; see Fig. 1), old  
 693 plantations (i.e. after threshold) and natural riparian forests

	Field edge		Riverbank	
	<i>F</i>	<i>Pr &gt; P</i>	<i>F</i>	<i>Pr &gt; P</i>
Light-demanding	31.15	< <b>0.0001</b>	32.75	< <b>0.0001</b>
Shade-tolerant	9.72	<b>0.0002</b>	0.47	0.6254
Non-natives	22.54	< <b>0.0001</b>	32.72	< <b>0.0001</b>
Natives	3.39	< <b>0.0001</b>	11.25	< <b>0.0001</b>
Wetland obligates	1.22	0.3010	3.40	<b>0.0394</b>
Wetland facultatives	0.98	0.3822	7.37	<b>0.0013</b>

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696

697

698 Table 2. Differences in the cover of vegetation strata between young plantations (i.e.  
 699 observations dated before threshold in species turnover; see Fig. 1), old plantations (i.e. after  
 700 threshold) and natural riparian forests

701

	Field edge		Riverbank	
	<i>F</i>	<i>Pr &gt; P</i>	<i>F</i>	<i>Pr &gt; P</i>
Trees	13.69	< <b>0.0001</b>	25.10	< <b>0.0001</b>
Shrubs	20.62	< <b>0.0001</b>	14.39	< <b>0.0001</b>
Dicots	1.23	0.2983	0.51	0.6040
Monocots	13.02	< <b>0.0001</b>	30.49	< <b>0.0001</b>
Ferns	0.10	0.9015	2.30	0.1084

702