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1 **The role of native woody species on the restoration of *campos rupestres* in quarries**

2
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14
15 **Abstract**

16 **Questions:** Can shrub and tree seedlings be reintroduced in an extremely harsh environment
17 by transplantation? Does the growth strategy of species affect their survival? What factors
18 influence the transplantation success? Do transplanted species influence their immediate
19 vicinity, e.g. promoting colonization by native species?

20 **Location:** *Campos Rupestres*, Espinhaço range, Minas Gerais, Brazil.

21 **Methods:** We studied the reintroduction of four native tree and 14 native shrub species. Their
22 transplantation success (survival, growth, and reproduction) and their impacts on their
23 immediate vicinity (understorey composition, soil surface indicators such as the cover of
24 moss, biological crust, bare ground, litter, herbaceous cover, and soil characteristics) were
25 assessed 4.5 years after transplantation.

26 **Results:** While some transplanted species had low survival (< 30%), half of them had a

27 survival >78% 4.5 years after transplantation. Plant growth was barely correlated to the
28 transplantation success in such harsh environment. Transplanted species did not influence soil
29 and understorey plant composition but significantly impacted soil surface indicators. The
30 shrub species with higher survival rates usually allowed the establishment of an understorey
31 herbaceous cover which may increase soil erosion control. This is also true for some species
32 for those the survival was <40%: *Diplusodon orbicularis* (survival: 39%) and *Lavoisiera*
33 *campos-portoana* (37%). Crown volume had a direct effect on light reaching the soil (e.g.
34 *Jacaranda caroba* or *Collaea cipoensis* had a less dense canopy more permeable to light
35 allowing understorey species). On the other hand, crown volume was positively correlated to
36 the amount of litter: Fabaceae species, such as *Chamaecrista semaphora* and *Mimosa*
37 *foliolosa*, had denser canopy and produced a thick layer of litter, limiting herbaceous species
38 establishment. Three tree species (*Enterolobium ellipticum*, *Kielmeyera petiolari*, and
39 *Zeyhera tuberculosa*) neither had high survival nor did facilitate the establishment of the
40 herbaceous cover. The layout and spacing of species and individuals must thus be considered
41 carefully to insure recolonization by native shrub and herbaceous species.

42 **Conclusion:** This study demonstrates the practical efficiency of some native species to restore
43 a harsh tropical ecosystem as the *campos rupestres* in terms of their transplantation success,
44 their effects on both the establishment of herbaceous species and soil conservation.

45
46 **Keywords:** assessment of restoration success; Cerrado; herbaceous understorey; neotropical
47 mountain grasslands; Serra do Cipó; transplantation success.

48 **Abbreviations:** Dret : *Dasyphyllum reticulatum* ; Jcar : *Jacaranda caroba* ; Abon:
49 *Actinocephalus bongardii*; Cfas: *Calliandra fasciculata*; Csem.: *Chamaecrista semaphora*,
50 Mfol.: *Mimosa foliolosa*; Ccip.: *Collaea cipoensis*; Dhir.: *Diplusodon hirsutus*; Dorb.:
51 *Diplusodon orbicularis*; Hbyr.: *Heteropterys byrsonimifolia*; Lcam.: *Lavoisiera campos-*
52 *portoana*; Mtax.: *Marcetia taxifolia*; Thet.: *Tibouchina heteromalla*; Lpac.: *Lafoensia pacari*;

53 Kpet.: *Kielmeyera petiolaris*; Eell.: *Enterolobium ellipticum*; Edys.: *Eugenia dysenterica*;
54 Ztub.: *Zeyhera tuberculosa*.

55 **Nomenclature:** Lista de Espécies da Flora do Brasil 2013 in <http://floradobrasil.jbrj.gov.br/>

56 **Running head:** *Campo rupestre* restoration

57

58 **Introduction**

59 Ecological restoration is the process of intentionally assisting the recovery of degraded
60 ecosystems in order to repair ecosystem processes, productivity and services, as well as to re-
61 establish the biotic integrity (SER 2004). Grassland restoration projects are often hampered
62 by abiotic constraints, such as increased soil nutrients in case of degradation by intensive
63 agriculture or the alteration of soil chemical and physical characteristics (i.e. limited nutrient
64 availability, low water availability) in case of degradation by quarrying and mining activities
65 (Ash et al. 1994, Jim 2001, Wong 2003, Yuan et al. 2006). Biotic constraints also affect
66 seedling establishment through the lack of reliable seed sources, the limited dispersal of
67 appropriate propagules or the presence of competitive exotic species (Ash et al. 1994,
68 Bradshaw 1997, Bakker & Berendse 1999, Wilson 2002, Shu et al. 2005).

69 Open ecosystems, such as grasslands or savannas, represent more than 31% of world
70 vegetation, but they have drastically decreased or have been highly altered throughout the
71 world over the last decades (Gibson 2009), due to intensification of agricultural practices
72 (Green 1990, Klink & Moreira 2002), land abandonment, invasive species, civil engineering
73 and changes in disturbance regimes (Hoekstra et al. 2005, Gibson 2009). These ecosystems
74 are important not only from the perspective of conserving biodiversity (FAO 1998), but also
75 in maintaining ecosystem services, such as increased water quality or decreased soil erosion
76 (Osborne et al. 1993, Berger & Rey 2004, MEA 2005 a, b). Moreover, since the process of
77 natural succession is slow after degradation, especially by quarrying and mining activities
78 (Bradshaw 1983, Davis et al. 1985, Bradshaw 1997), their restoration is often attempted.

79 The Cerrado is the richest tropical savanna in the world, representing the second
80 largest vegetation formation of Brazil originally covering c.a. 2.2 million km² or 23% of the
81 country (Oliveira & Marquis 2002) and due to anthropogenic pressures (e.g. intensive
82 agriculture, mining, quarrying) is currently one of the most endangered biomes in South
83 America (Klink & Machado 2005, Hoekstra et al. 2005). This has led to biodiversity losses,
84 landscape fragmentation, biological invasions (Pivello et al. 1999), soil erosion, water
85 pollution and land degradation (Klink & Moreira 2002). *Campos rupestres* are one of the
86 physiognomies of the Cerrado biome, and are usually found above 900 meters high in
87 altitude. They are composed of a more or less continuous herbaceous stratum with
88 sclerophyllous evergreen shrubs and small trees growing between rocky outcrops, supporting
89 a high biodiversity with one of the highest levels of endemism in Brazil (Giulietti et al. 1997,
90 Carvalho et al. 2012). Such ecosystem is under extreme environmental conditions; their soils
91 are coarse textured and shallow, with high Al³⁺ and low nutrient content (Benites et al. 2007).
92 Few studies have been carried on such physiognomies of the Cerrado and they remain poorly
93 documented while restoration ecology studies are urgently needed.

94 According to the level of degradation, restoration of quarries and mines may require
95 seed addition (Cooper & MacDonald 2000, Turner et al. 2006, Kirmer et al. 2012, Ballesteros
96 et al. 2012), native species transplants (Ash et al. 1994, Soliveres et al. 2012), turves or
97 rhizomes transfer (Ash et al 1994, Cooper & MacDonald 2000). Currently in Brazil, many
98 mine and quarry mitigation projects use exotic species for revegetation, such as the African
99 grass *Melinis minutiflora* (Griffith & Toy 2001), to rapidly reach specific goals, e.g. to reduce
100 soil erosion. Exotic species are one of the major threats to local diversity, particularly when
101 degraded areas are close to roads where propagation and invasion risks are higher (Hansen &
102 Clevenger 2005; Barbosa et al. 2010).

103 Spontaneous regeneration of woody as well herbaceous campo rupestre species does
104 not seem to occur on degraded *campos rupestres* or is extremely slow (Le Stradic 2012) in

105 contrast with the seasonal deciduous forests (Sampaio et al 2007). Several non-mutually-
106 exclusive hypotheses could explain the lack of spontaneous recruits in degraded areas
107 (Bradshaw 2000): i) species produce viable seeds but they do not disperse far enough to reach
108 degraded sites; ii) dispersed seeds arrive to degraded areas but do not germinate due to the
109 high temperature and dryness of the bare and nutrient poor and/or toxic substrate; iii)
110 dispersed seeds are able to germinate but further development of saplings does not take place
111 due to the extreme harshness of the degraded site, the stress caused by natural enemies, or
112 lack of symbiotic interactions with facilitating arbuscular mycorrhizal fungi. The first two
113 reasons and sometimes the third one can be overcome by reintroduction which consists in the
114 re-establishment of taxa in part of their native range from where they had disappeared or had
115 drastically declined (Maunder 1992; Young 2000). Transplantation of native species may thus
116 be a suitable substitute (Maunder 1992; Bradshaw 1997, Byers et al. 2006, Hölzel et al. 2012),
117 ensuring that a desired panel of species are introduced and avoiding limited seedling
118 establishment (Bradshaw 1997).

119 For practical reasons, restoration by reintroduction often involves a single species;
120 restoring full communities is often costly and difficult to implement (Sampaio et al. 2007).
121 Usually species are selected as they are keystone, structuring, dominant or rare species
122 (Maunder 1992; Byers et al. 2006). Recent interest in the outstanding biodiversity of *campos*
123 *rupestres* has led to germination studies of some native plants which is a necessary step to
124 perform restoration projects (Gomes et al. 2001, Silveira et al. 2012). Species propagation and
125 their performance under controlled conditions in greenhouses represented the next crucial step
126 for restoration programs (Negreiros et al. 2009). The third step consists in a pilot field study.

127 It is now widely accepted that monitoring should be carefully planned prior, during
128 and after all restoration projects (Holl & Cairns 2002). In order to provide a common basis for
129 the assessment of restoration success, numerous measurements (i.e. ecosystem attributes)
130 were proposed (SER 2004). However, most projects consider one or two measurements

131 among the three major ecosystem attributes: (1) species diversity; (2) vegetation structure;
132 and (3) ecological processes (Ruiz-Jaen & Aide 2005). When restoration projects are based on
133 (single-) native species reintroduction, monitoring and evaluation of success is often restricted
134 to survival and growth of these reintroduced species (Maunder 1992; Guerrant & Pavlik
135 1998). Nevertheless, introduced species can drastically change ecosystem functioning
136 (Simberloff et al. 2005) and monitoring should therefore assess the impact of introduced
137 species on their environment (SER 2004); 1) by measuring reintroduced species survival,
138 growth and recruitment ability and 2) by measuring the impacts of reintroduced species on
139 their direct environment. While short-term monitoring is needed to document the survival and
140 establishment of reintroduced species, mid-term and long-term monitoring is essential to
141 understand induced changes in ecosystem functioning (Maunder 1992; Sutter 1996).

142 In this context, we studied the reintroduction of 18 native *campo rupestre* tree and
143 shrub species to degraded areas. The questions raised by this study were: (1) can shrub and
144 tree seedlings be reintroduced in an extremely harsh environment by transplantation? ; (2)
145 does the growth strategy of species affect their survival?; (3) what factors influence the
146 transplantation success?; and finally (4) do transplanted species influence their environment,
147 i.e. the herbaceous understorey, the soil properties, and the soil surface indicators in their
148 immediate vicinity? In this experiment, we expected the ideal to-be-transplanted species to be
149 able to survive and to grow on harsh environments and to allow herbaceous species,
150 cryptogams and biological crust to colonize the understorey in order to increase total
151 vegetation cover and thus soil conservation.

152

153 **Methods**

154 **STUDY SITE**

155 *Campos rupestres* are encountered along the Espinhaço mountain range (states of
156 Minas Gerais and Bahia) in Brazil. Our study area is located in the southern portion of the

157 Espinhaço Range. Fieldwork was conducted in the Vellozia Private Reserve (19°16'45.7"S,
158 43°35'27.8"W; elevation 1200 m) in the buffer zone of the Serra do Cipó National Park
159 (Minas Gerais). The climate is classified as Cwb according to the Köppen's system, which is
160 characterized by warm temperature, dry winter and warm summer. It is markedly seasonal,
161 with a rainy season during summer. The mean annual precipitation is 1622 mm and the annual
162 temperature is 21.2°C (Madeira & Fernandes 1999).

163 A study reported the presence of degraded areas along the highway MG010 in 1996 (Negreiro
164 et al. 2011) which dated back from 1990. They were exploited for gravel and/or were used to
165 park machines. These small quarries are common in the region: vegetation is destroyed and
166 soils are disturbed and when exploitation stops, soils are not returned entirely and
167 construction debris may be added resulting in a high-altered soil. All of these degraded areas
168 are surrounded by pristine *campos rupestres*, that is why we chose them as the reference
169 ecosystem. Two experimental degraded areas, with a sandy altered substrate, were selected.
170 Sites were located a few tens of meters apart, thus, for both sites, exploitation stop at the exact
171 same time and the mixed soil horizons were put back in the same way in order to have true
172 site replicates. Indeed, sites further apart may have different soil granulometry due to the way
173 that soil horizons are mixed after exploitation.

174

175 EXPERIMENTAL DESIGN

176 Eighteen native species were planted: fourteen shrub species and four tree species
177 (Table 1). In 2002, seeds of all eighteen species were gathered in the field in areas
178 surrounding the degraded areas. Mature fruits were collected from at least ten individuals of
179 each species. For *Chamaecrista semaphora*, *Mimosa foliolosa*, *Collaea cipoensis* and
180 *Enterolobium ellipticum*, seed dormancy was broken by mechanical scarification (Gomes et
181 al. 2001). In November 2002, seeds were hydrated for 24 hours and each seed was sown in
182 black polythene bags (8cm diameter and 20cm deep) directly in the substrate, composed of

183 1/3 of soil from around the degraded areas, 1/3 of peat and 1/3 of organic compost of confined
184 cattle dung. To correct for soil acidity and nutrients, 2L dolomitic limestone and 1L NPK
185 (4:14:8) were added for 360L of substrate. Seedlings were placed in a greenhouse: 50% light,
186 watering by micro-sprinklers for 15 minutes, three times a day, equivalent to 17.5 mm/day. At
187 the end of April 2003, seedlings were transferred out of the greenhouse and exposed to
188 ambient conditions, while watering by micro-sprinklers was gradually reduced.

189 Between 20 Jul 2003 and 26 Jul 2003, we randomly assigned 64 eight month-old
190 seedlings (except *Lavoisiera campos-portoana*: 27 months-old) of each species to be
191 transplanted to the degraded areas. Shrubs were transplanted on both degraded areas; while
192 trees were transplanted on only the largest degraded area. Seedling transplantation was
193 carried out according to the experimental design explained in Figure 1. As planting was
194 carried out during the dry season, plants were irrigated by sprinklers during the first two
195 months. Plants received water for 15 minutes at every other 10 days.

196

197 MONITORING OF THE SURVIVAL AND GROWTH OF PLANTED SPECIES

198 Survival was recorded for each individual in August 2003 (date of transplantation),
199 September 2003, February 2004, April 2006 and February 2008 (4.5 years after
200 transplantation). Some individuals were considered dead one year, but they had to be
201 considered alive after due to resprouting. At each date, growth was evaluated by measuring
202 the height of the main stem, crown volume (calculated using the largest crown diameter, the
203 largest perpendicular diameter to the first one and crown height) and basal diameter of each
204 individual. These variables are known to reflect the growth of both roots and shoot systems
205 (Niklas 1993; Negreiros et al. 2009). Relative Growth Rates (RGRs) were calculated for
206 diameter, height and volume as: $RGR = (\ln x_{t_j} - \ln x_{t_i}) / (t_j - t_i)$ where x denotes the variable
207 measured at two different dates t_i and then t_j . Since it is important to assess the sustainability

208 of a species in a restored area through its reproductive ability, we recorded the occurrence of
209 new sprouts, individuals with flowers or fruits and new seedlings in February 2008.

210

211 UNDERSTOREY AND SOIL SAMPLING

212 In February 2008, on each plot, four 20×20cm quadrats were set randomly to assess
213 soil surface indicators and the composition of species colonizing the understorey (understorey
214 composition and richness). Percent of cover of each understorey species was recorded.
215 Monitored soil surface indicators were: (I) cover of moss (%); (II) biological crusts (thin
216 organic layer formed by cyanobacteria, green algae, lichens, fungus and heterotrophic bacteria
217 (Belnap & Lange 2001)); (III) cover of bare ground (%); (IV) litter cover (%); and (V)
218 herbaceous plant cover (%) (hereafter named herbaceous cover). In order to assess the
219 influence of transplanted species on light reaching the ground, canopy closure (named shade)
220 was estimated based on the vertical projection of the crown area weighted by an index of
221 foliage density (Daubenmire 1959). This index was calculated from the analysis of four
222 canopy pictures for each species using an image processing software which assessed the
223 percentage of the picture with foliage.

224 In order to determine whether species influence soil chemical properties, one soil
225 sample was collected on each plot, resulting from four sub-samples which were mixed and
226 homogenized, dried and sieved prior to chemical analyses. The following chemical analyses
227 were performed: P and K in mg/dm³, N and C in dag/kg, Mg²⁺, Al³⁺, Ca²⁺ in cmol_c/dm³,
228 Organic Matter (OM) in dag/kg – P, Na, K with the Mehlich 1 extraction method, Ca²⁺, Mg²⁺,
229 Al³⁺ with 1 mol/L KCl extraction, OM = C.Org x 1.724 following the Walkley-Black
230 method).

231

232 DATA ANALYSIS

233 The effects of the qualitative variables “sites” and “plots” on survival (0 or 1 at the individual
234 level) at the end of the survey were tested using GLM (Generalized Linear Models) with a
235 binomial distribution and a logit link function (Crawley 2007). Then, the effect of the
236 variables “initial size of individuals” (size when transplanting) and “RGR” on individual
237 survival were analyzed with GLM procedures (binomial distribution and logit link function)
238 by setting the “plot” and “site” effects as an *offset* component of the GLM. An *offset* specifies
239 an *a priori* known component to be included in the linear predictor during fitting (using the R
240 package stats) (Crawley 2007). Differences in survival according to the plant family and plant
241 stature levels were tested at the different times of the survey (2004, 2006 and 2008) using χ^2
242 tests.

243 Similar treatments being expected to lead to similar effects in both sites, multivariate
244 analyses were performed to assess the co-structure of their variables. Three co-inertia
245 analyses were thus ran between site 1 and 2 considering: (i) soil surface indicators (2 matrices
246 of 30 plots \times 6 soil surface indicator), (ii) soil chemistry (2 matrices of 30 plots \times 9 soil
247 variables) and understorey composition data (2 matrices of 30 plots \times 81 understorey species)
248 separately (Chessel et al. 2009). The significance of the coinertia coefficient was estimated
249 with 999 Monte Carlo permutations.

250 Then, as a co-structure was found only for soil surface indicators, we further explored
251 the effects of transplanted species on these indicators, by running an inter-class Principal
252 Component Analysis (76 transplanted and control plots \times 6 soil surface indicators; PCA-
253 between; ade4 R package, Chessel et al. 2009). Simple ANOVAs, followed by post-hoc tests
254 (Tukey HSD: Honestly Significant Difference) were performed: herbaceous cover and
255 understorey richness were treated as dependent variables and species and control plots as
256 categorical predictors. Normality and homoscedasticity assumptions were checked and a
257 square root transformation was applied (Sokal & Rohlf 1998). Species morphology especially
258 the crown volume was expected to impact on the amount of light reaching the soil. In order to

259 assess the relationship between crown volume at the end of the survey and soil surface
260 indicators, tests for association between paired samples using Spearman's ρ were carried out.
261 All statistical analyses were performed using the software R (R Development Core Team
262 2009).

263

264 **Results**

265 SURVIVAL AND GROWTH OF PLANTED SPECIES

266 Differences in terms of survival and growth were observed. Four and a half years after
267 transplantation, some species were characterized by a fairly high survival (above 78%):
268 *Calliandra fasciculata*, *Collaea cipoensis*, *Jacaranda caroba*, *Dasyphyllum reticulatum*,
269 *Heteropterys byrsonimifolia*, *Tibouchina heteromalla*, *Eugenia dysenterica*, *Diplusodon*
270 *hirsutus* and *Lafoensia pacari*. On the contrary survival was lower than 50% for
271 *Actinocephalus bongardii*, *Chamaecrista semaphora*, *Diplusodon orbicularis*, *Enterolobium*
272 *ellipticum*, *Lavoisiera campos-portoana* and *Zeyhera tuberculosa* (Table 2). In addition,
273 survival of seven species significantly differed depending on the plot and/or the site: *A.*
274 *bongardii*, *C. fasciculata*, *C. semaphora*, *D. hirsutus*, *D. orbicularis*, *J. caroba* or *Kielmeyera*
275 *petiolaris*. Individuals growing in the site 2 generally presented a higher survival (Table 2).

276 Beyond their simple survival, some species were able to colonize available sites:
277 *Chamaecrista semaphora*, *C. cipoensis*, *Marcetia taxifolia* and *M. foliolosa* recruited more
278 than 10 seedlings. Others expanded through resprouting, such as the majority of individuals of
279 *C. cipoensis*, *D. reticulata*, *D. hirsutus*, *H. byrsonimifolia*, *L. pacari*, and *T. heteromalla*
280 (Table 2). Finally no signs of reproduction were observed in *Z. tuberculosa*, *E. dysenterica*
281 and *E. ellipticum* (Table 2).

282 Species appeared to differentially survive according to their families at different dates
283 (respectively $\chi^2=319.8$, $df=4$, $P<0.001$ in 2006, $\chi^2=21.8$, $df=4$, $P<0.001$ in 2008).
284 Melastomataceae suffered higher mortality (at least of the aboveground parts) than the other

285 families at the beginning and during the first years, as 39% of their individuals died during the
286 first six months and 76% after 2.5 years, especially *L. campo-portoana* (Table 2 & Table 3).
287 Melastomataceae species were able to resprout, thus increasing their survival rates 4.5 years
288 after the transplantation (Table 3) compared to the two first years after the transplantation. At
289 the end of the survey, Fabaceae and Bignoniaceae were the families with the highest mortality
290 rate (respectively 59.69% and 54.69% of survival) (Table 3). Shrubs presented higher
291 mortality than trees at the beginning and during the first years of the transplantation
292 (respectively 10% vs. 6% respectively for 2004; $\chi^2=3.7$, $df=1$, $P=0.052$ and 29% vs.14%
293 respectively for 2006; $\chi^2=21.9$, $df=1$, $P<0.001$), while at the end of the survey shrubs were
294 characterized by a lower mortality than trees (31% vs. 45% respectively; $\chi^2=15.6$, $df=1$,
295 $P<0.001$).

296 For most species, the RGR did not appear to significantly reflect the final survival
297 probability. However, when such effects were observed, a faster growth was associated with
298 a higher survival, excepted for *C. semaphora* (Table 4). Survival 4.5 year after the
299 transplantation was positively related to the initial size of individuals for *A. bongardii*, *D.*
300 *reticulatum* and *M. taxifolia* and to a lesser extent for *E. dysenterica* and *C. fasciculata* (Table
301 4). For only two species, *E. ellipticum* and *M. taxifolia*, the survival 6 months after the
302 transplantation was positively related to the RGR during the first month (Table 4). The RGR
303 during the first 6 months was positively linked to the survival 2.5 years after the
304 transplantation (in 2006) for five species: *C. fasciculata*, *D. orbicularis*, *K. petiolaris*, *M.*
305 *taxifolia* and *M. foliolosa*. Finally, for just three species, *C. fasciculata*, *D. reticulatum* and *Z.*
306 *tuberculosa*, the RGRs during the first years, between 2004 and 2006, were positively
307 correlated with the survival at the end of the survey, 4.5 years after the transplantation, while
308 it was negatively correlated with the survival of one species: *C. semaphora* (Table 4).

309

310 UNDERSTOREY RECOLONISATION

311 Similar treatments should lead to similar effects; we then expected that the factor
312 “species” lead to some co-structure between the two sites. However among the three co-
313 inertia analyses run between site 1 and 2, a significant co-structure was found only for soil
314 surface indicators ($RV=0.390$, $P<0.05$ Monte-Carlo permutations), and not for soil or
315 understorey composition data ($RV=0.136$, $P=0.17$ and $RV=0.595$, $P=0.34$ respectively). A first
316 PCA was carried out and indicated that *C. semaphora* was highly correlated with percent
317 cover of litter masking other effects (Inertia = 0.42, $P<0.001$ - Monte-Carlo permutations).
318 Another PCA was thus carried out, without *C. semaphora* (Inertia = 0.35, $P <0.01$ - Monte-
319 Carlo permutations), indicating on the axis 1 (45% of the total inertia) that *Eugenia*
320 *dysenterica* (8%), *Z. tuberculosa* (9%) and *K. petiolaris* (10%) were characterized by bare
321 ground (axis contribution: 23%) while *C. fasciculata* (29%) *M. foliolosa* (26%) and *L.*
322 *campos-portoana* (9%) were correlated with high cover of litter and shade (axis contribution:
323 38% and 34% respectively) (Fig. 2). Axis 2 (38% of the total inertia) underlined that
324 *Actinocephalus bongardii* (6%), *D. hirsutus* (10%), *L. campos-portoana* (13%) and control
325 plot (27%) were characterized by a dense cover of biological crust (39%) and to a lesser
326 extent by a cover of moss (11%) and herbaceous vegetation (18%) contrary to *E. ellipticum*
327 (8%) and *K. petiolaris* (10%) which were distinguished by a higher cover of bare ground
328 (21%).

329 The transplanted species appeared to influence both species richness and the
330 herbaceous cover of the understorey. *Calliandra fasciculata*, *J. caroba*, *D. reticulatum*, *D.*
331 *orbicularis*, *L.campos-portoana*, *A. bongardii* and control plots had significantly higher
332 understorey richness than that of other species ($F=3.33$, $P<0.001$). Moreover the pre-cited
333 species as well as *D. hirsutus*, *C. cipoensis* and control plots had significantly higher
334 herbaceous cover than that of other species ($F = 2.78$, $P<0.001$). The floristic survey of the
335 herbaceous understorey led to the identification of 69 species, of which the majority were
336 represented by ruderal species which were likely to be dispersed from the road and that did

337 not occur on the surrounding savannas. The most represented family was Poaceae (21
338 species), followed by Fabaceae (15) and Asteraceae (8). Two invasive species were identified:
339 *Melinis repens* (from Africa; Starr et al. 2006) and *Euphorbia hirta* (from India, USDA
340 2008).

341 Crown volume, was positively correlated with the cover of litter (Spearman's $\rho=0.65$,
342 $P<0.01$) and, since it influenced the amount of light reaching the soil, with shade (Spearman's
343 $\rho=0.74$, $P<0.001$). Crown volume was negatively correlated with the cover of bare ground
344 (Spearman's $\rho=-0.54$, $P<0.05$). No significant correlations between crown volume and
345 biological crust, moss and herbaceous cover were found.

346

347 **Discussion**

348 The restoration success typically depends on multiple criteria. In this survey of a
349 transplantation experiment, we considered two crucial aspects: (i) the capacity of transplanted
350 species to settle and reproduce in the degraded area; (ii) the effect of the re-introduced species
351 on their immediate environment which may result in an increased re-colonization of the site
352 by other species. This study represents a landmark in the restoration of this type of tropical
353 mountain savannas. We report one of the first conclusive restoration projects on these highly
354 threatened ecosystems and emphasise that transplantation in degraded sites is a very good
355 way to reintroduce native species and increase plant cover in harsh environments.

356

357 SURVIVAL AND GROWTH OF PLANTED SPECIES

358 Prior to the analysis of the efficiency of transplanted species to modify their
359 environment, the first step in restoration using transplants is to identify species characterized
360 by a high survival. Although some native species transplanted in this study was characterized
361 by a low survival (<50%), half of our species panel showed a high survival (>78%) 4.5 years
362 after transplantation in highly degraded areas. Those species, *C. fasciculata*, *C. cipoensis*, *J.*

363 *caroba*, *D. reticulatum*, *H. byrsonimifolia*, *T. heteromalla*, *E. dysenterica*, *D. hirsutus* and *L.*
364 *pacari*, are therefore excellent candidates to restore degraded areas of highland savannas.
365 While native trees presented a low survival compared to the native shrubs, the tree species *E.*
366 *dysenterica* was also successfully transplanted (survival > 96%) and could be reintroduced
367 with success, even if its contribution to recruitment would probably occur in the longer term.

368 Beyond survival, planted species, were able to reproduce vegetatively and/or sexually
369 and therefore initiate the self-recolonisation of the degraded sites. This was also true
370 concerning some species presenting low survival and in another hand 1) which are able to
371 recruit numerous seedlings, such as the Fabaceae species: *Mimosa foliolosa* or *Chamaecrista*
372 *semaphora*, or, 2) which are able to resprout like Melastomataceae species. This is
373 particularly interesting since most of the transplanted species do not seem to fastly re-colonize
374 degraded sites. They are not generally found in disturbed areas which have been abandoned
375 for years (Le Stradic 2012), and their seeds are not detected in the seed bank (Medina &
376 Fernandes 2007).

377 In addition, species lifespan should balance any evaluations exclusively based on the
378 survival of transplanted individuals. *Actinocephalus bongardii* presented the lowest survival
379 of all planted species (< 10%), but this species commonly lives only three to four years
380 (Oriani et al. 2008) and the transplanted individuals survived well during the first two years.
381 *Actinocephalus bongardii* has bloomed every year and has produced a large number of seeds
382 although few recruitments are currently found. *A. bongardii* thus participated in degraded
383 area stabilization during the first years. Moreover, dead individuals produced a fine litter
384 which may have played a role in increasing soil organic matter and nutrients and in allowing
385 colonisation by herbaceous species.

386 Plant growth did not appear to be a generic predictor of individual survival. Early
387 survival, reflecting the species ability to establish on degraded sites, was poorly related to
388 early RGR. In the same way, for only five species, i.e. *C. fasciculata*, *D. orbicularis*, *D.*

389 *hirsutus*, *K. petiolaris*, *M. foliolosa* and *M. taxifolia*, the growth rate partially reflected the
390 ability of an individual to persist in degraded areas. In a majority of the species, survival at
391 the end of the survey was not related to the RGR measured on shoots which might be the
392 result of an investment in root growth.

393 However, if growth is not a critical factor determining the survival in degraded areas,
394 we can expose some hypotheses explaining the low survival of some species. First edaphic
395 conditions on degraded sites are more stressful than on their non-degraded counterparts.
396 Abiotic conditions could limit the early stage of plant establishment (Maestre et al. 2006);
397 maladjustment to the physical and chemical conditions of the degraded sites, critical in the
398 short-term, may lead to a high mortality during the early stage (e.g., as observed for
399 Melastomataceae). Establishment of tree and shrub seedlings in Neotropical savannas is
400 highly constrained by drought, fire and competition with herbaceous species and thus depends
401 on seedling ability to access water (Medina & Silva 1990).

402 In addition, on degraded sites, species distribution is less dense which modify species
403 interactions compared to pristine areas. Fabaceae species bring, for the plant community, the
404 potentially important feature of fixing atmospheric nitrogen. Unfortunately, two tested
405 Fabaceae (*M. foliolosa* and *C. semaphora*) recorded high late mortality, possibly due to the
406 effects of intra-specific competition occurring at the relatively small experimental plot scale.
407 In a different way, *Enterolobium ellipticum* recorded a high mortality rate during the last year
408 due to the parasitism of all individuals by *Struthanthus flexicaulis* Mart. (Loranthaceae).

409

410 COMMUNITY RESTORATION

411 Candidate species for future restoration projects can be listed on the basis of survival
412 but the next step must be to assess the efficiency of transplanted species to modify their
413 environment (i.e. nurse species, Padilla & Pugnaire 2006). Our work shows that transplanted
414 species, even if they did not significantly influence soil properties and understorey plant

415 composition, affected significantly their immediate vicinity modifying soil surface indicators,
416 potentially increasing the establishment of recruits or future colonization by other species. A
417 large fraction of our species (i.e. *C. fasciculata*, *C. cipoensis*, *J. caroba*, *D. reticulatum*, *D.*
418 *orbicularis*, *D. hirsutus* *L. campos-portoana* and *A. bongardii*) allowed the establishment of
419 an herbaceous strata participating to the soil stabilisation. We, however, did not find a
420 potential nurse effect of our species, as an equal herbaceous cover was also present on control
421 plots. In addition, large part of the new herbaceous cover is composed by ruderal species,
422 which were not encountered on pristine highland savannas, underlining the real limitation of
423 savanna species to immigrate on degraded areas.

424 Colonization of the understorey by herbaceous species is partly influenced by the
425 amount of light reaching the ground and therefore by the canopy density and morphology of
426 transplanted shrubs and trees. *Jacaranda caroba* and *C. cipoensis* have a canopy which is
427 more permeable to light. They thus favour colonisation by herbaceous species, by contrast
428 with *C. semaphora*. Canopy opening influences regeneration of herbaceous understorey under
429 tree and shrub cover (Cusack & Montagnini 2004; Hobbs & Mooney 1986), especially since
430 savannah species are not shade tolerant (Hoffmann & Franco 2003).

431 Denser plant cover should increase soil stability (Snelder & Bryan 1995) but according
432 to Rey (2003) vegetation cover of 30% is already effective to control erosion and to trap
433 sediments. *Marcetia taxifolia*, characterized by an average cover of the herbaceous
434 understorey ($23.8\% \pm 7.3$), has significant cryptogam cover ($30\% \pm 9.5$) which also
435 participates in erosion control. The ground does not necessarily have to be covered with
436 shrubs; if their establishment is promoted, biological crusts and cryptogams can also play a
437 major role in erosion control (Belnap & Lange 2001).

438 On the contrary, we highlighted that some species can limit re-colonisation by
439 understorey species. For example, in this study, we showed that Fabaceae species (i.e. *C.*
440 *semaphora*, *M. foliolosa*, *C. fasciculata*) were characterized by a high production of a thick

441 litter. Leaves of plants of the genus *Chamaecrista* are rich in secondary compounds such as
442 tannins (e.g. Madeira et al. 1998); tannin-rich litter decomposes very slowly and it has been
443 shown that grasses may be sensitive to tannins released during leaf decomposition (Facelli
444 1991). This litter thus induced a strong inter-specific competition not favourable to
445 colonisation by herbaceous understorey. In addition species of the genus *Mimosa* are often
446 competitive (Braithwaite et al. 1989; IUCN 2002) due to their architecture, dense foliage and
447 the shade they create.

448 A bad planting protocol can thus also lead to some re-colonization limitation, beyond a
449 higher mortality by intra-specific competition, as we have just mentioned with the example of
450 Fabaceae which should be planted far apart from one another due to their plant architecture
451 and physiology. Therefore, when designing planting protocols, intra- and inter-specific
452 competition and the effects of shade and litter have to be taken into account. To increase bare
453 ground colonization by herbaceous species, plantation should be spaced out, as previously
454 stated, and various types of plant architecture must be combined.

455

456 **Conclusion**

457 This work shows that the reintroduction of native species into a harsh environment is possible
458 using seedling transplantation. Species, such as *C. fasciculata*, *C. cipoensis*, *J. caroba*, *D.*
459 *reticulatum* and *D. hirsutus*, are excellent candidate to restoration project since they were able
460 to settle and reproduce in the degraded area and they allowed the re-colonization of the site by
461 understorey species. Our work emphasise that plant growth did not seem a good criterion to
462 determine the transplantation success in such harsh environment. Intra-specific competition,
463 leading to higher mortality, was observed especially for Fabaceae species. Therefore, a
464 particular attention should be taken when planning restoration. A suitable planting design,
465 including space between competitive species, is necessary to avoid mortality due to
466 competition and to allow recolonisation.

467 Botanical and ecological knowledge of these ecosystems is still poor and needs to be
468 improved in order to provide a better basis for selection of species to be transplanted.
469 Monitoring is important to measure herbaceous understorey colonization (herbaceous, moss
470 or biological crust cover and richness of herbaceous understorey) and to assess the efficiency
471 of recruitment of transplanted species. Long-term monitoring is necessary; the influence of
472 transplanted species on soil properties and understorey plant composition might occur on a
473 longer time.

474

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480

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672 **Table 1:** List of transplanted species. Abbrev: abbreviations used in tables and figure. Stature: is the stature of
 673 the plant in the study. *Actinocephalus bongardii* is an herb but was considered as a shrub due to its stature
 674

Species	Abbrev.	Family	Stature
<i>Dasyphyllum reticulatum</i> (DC.) Cabrera	Dret	Asteraceae	Shrub
<i>Jacaranda caroba</i> (Vell) A. DC.	Jcar	Bignoniaceae	Shrub
<i>Actinocephalus bongardii</i> A. St.-Hil Sano	Abon	Eriocaulaceae	Shrub
<i>Calliandra fasciculata</i> Benth. var. <i>bracteosa</i> (Bentham) Barneby	Cfas	Fabaceae	Shrub
<i>Chamaecrista semaphora</i> HS. Irwin & Barneby	Csem	Fabaceae	Shrub
<i>Mimosa foliolosa</i> Benth. ssp. <i>pachycarpa</i> (Bentham) Barneby var. <i>pachycarpa</i>	Mfol	Fabaceae	Shrub
<i>Collaea cipoensis</i> Fortunato	Ccip	Fabaceae	Shrub
<i>Diplusodon hirsutus</i> (Cham & Schlecht) DC	Dhir	Lythraceae	Shrub
<i>Diplusodon orbicularis</i> Koehne	Dorb	Lythraceae	Shrub
<i>Heteropterys byrsonimifolia</i> A. Juss	Hbyr	Malpighiaceae	Shrub
<i>Lavoisiera campos-portoana</i> Mell. Barr	Lcam	Melastomataceae	Shrub
<i>Marcetia taxifolia</i> A. St.-Hil DC	Mtax	Melastomataceae	Shrub
<i>Tibouchina heteromalla</i> (D. Don) Cogn.	Thet	Melastomataceae	Shrub
<i>Lafoensia pacari</i> A. St.-Hil	Lpac	Lythraceae	Shrub
<i>Kielmeyera petiolaris</i> Mart.	Kpet	Clusiaceae	Tree
<i>Enterolobium ellipticum</i> Benth.	Eell	Fabaceae	Tree
<i>Eugenia dysenterica</i> DC.	Edys	Myrtaceae	Tree
<i>Zeyhera tuberculosa</i> Bureau	Ztub	Bignoniaceae	Tree

675 **Table 2:** Overall and site-specific survival (%) in February 2008. Reproduction was recorded as the percentage
676 of individuals with flowers and/or fruits, the number of seedlings recruiting and the percentage of individuals
677 using vegetative reproduction. For species abbreviations, see Table 1. Site and plot effects were assessed using
678 GLM procedures. / : no data, empty cell: non-significant, *: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$ (2 plots in
679 each site with 16 plants in each plot)

Species	Survival 2008 (%)		Site effect	Plot effect	Individuals with flowers or/and fruits (%)	Number of seedlings recruiting for 64 transplanted plants	Individuals using vegetative reproduction (%)
	Overall	(Site 1 - Site 2)					
Lafoensia pacari	100	(100.0 - 100.0)			0	0	100
Eugenia dysenterica	96.9		/		0	0	0
Heteropterys byrsonimifolia	96.9	(100.0 - 93.8)			0	0	96.9
Tibouchina heteromalla	96.9	(96.9 - 96.9)			32.8	1	95.3
Dasyphyllum reticulatum	89.1	(87.5 - 90.6)			39.1	1	89.1
Collaea cipoensis	82.8	(90.6 - 75.0)			46.9	10	82.8
Calliandra fasciculata	81.3	(65.6 - 96.9)	***	**	40.6	3	0
Jacaranda caroba	81.3	(84.4 - 78.1)		**	0	1	0
Diplusodon hirsutus	78.1	(62.5 - 93.8)	**	***	34.4	0	78.1
Kielmeyera petiolaris	67.2		/	**	6.3	0	0
Marcetia taxifolia	60.9	(56.3 - 65.6)			53.1	15	0
Mimosa foliolosa	59.4	(65.6 - 53.1)			40.6	11	0
Chamaecrista semaphora	46.9	(28.1 - 65.6)	**	*	46.9	15	0
Diplusodon orbicularis	39.1	(25.0 - 53.1)	*	*	12.5	2	0
Lavoisiera campos-portoana	37.5	(28.1 - 46.9)			29.7	0	37.5
Enterolobium ellipticum	28.1		/		0	0	0
Zeyhera tuberculosa	28.1		/		0	0	0
Actinocephalus bongardii	10.9	(18.8 - 3.1)	*	*	9.4	1	0

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681

682 **Table 3:** Number and percentage of dead individuals in 2004, 2006 and 2008 according to their families.
 683 Resprouting individuals were taken into account, which increased survival rate for some families (e.g.
 684 Melastomataceae species)

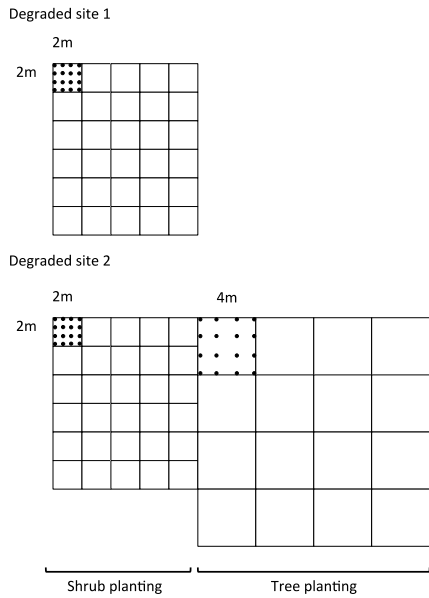
2004	Number of dead individuals	% of survival	Total number of individuals
Other families	8	97.50%	320
Bignoniaceae	0	100.00%	128
Fabaceae	11	96.56%	320
Lythraceae	11	94.50%	200
Melastomataceae	75	60.94%	192
2006			
Other families	40	87.50%	320
Bignoniaceae	9	92.70%	128
Fabaceae	60	81.25%	320
Lythraceae	39	80.50%	200
Melastomataceae	146	23.06%	192
2008			
Other families	89	72.19%	320
Bignoniaceae	58	54.69%	128
Fabaceae	129	59.69%	320
Lythraceae	53	73.50%	200
Melastomataceae	67	65.10%	192

685 **Table 4:** Effects of the early RGR (between August 2003 and September 2003), the mid-term RGR (between September 2003 and February 2004) and the late RGR (between
686 February 2004 and April 2006) on respectively the survival in 2004, 2006 and 2008, using GLM procedures. Effects of the initial plant size (diameter, height and volume in 2003) on
687 the survival in 2008 using GLM procedures. / : no data, empty cell: non-significant, +: significant positive GLM coefficient value with $P < 0.05$, ++: with $P < 0.01$, +++: with $P <$
688 0.05 , --: significant negative GLM coefficient value with $P < 0.01$, ---: with $P < 0.001$

Species	Effect of early RGR on survival in 2004 (transplantation + 6 months)			Effect of mid RGR on survival in 2006 (transplantation + 2.5 years)			Effect of late RGR on survival in 2008 (transplantation + 4.5 years)			Effect of initial plant size on survival in 2008		
	Diameter	Height	Volume	Diameter	Height	Volume	Diameter	Height	Volume	Diameter	Height	Volume
Abon											+	+
Cfas					+	+		++	+++	+		
Csem							---					
Ccip												
Dret							++	+++	++	+		+
Dhir						+						
Dorb				++	++	+++						
Eell	+											
Edys										+		
Hbyr												
Jcar												
Kpet				+		++						
Lpac												
Lcam				/	/	/	/	/	/			
Mtax	+++		++	++	+++	+++					+	+
Mfol				+++	+++	+++						
Thet							/	/	/			
Ztub							+++	+				

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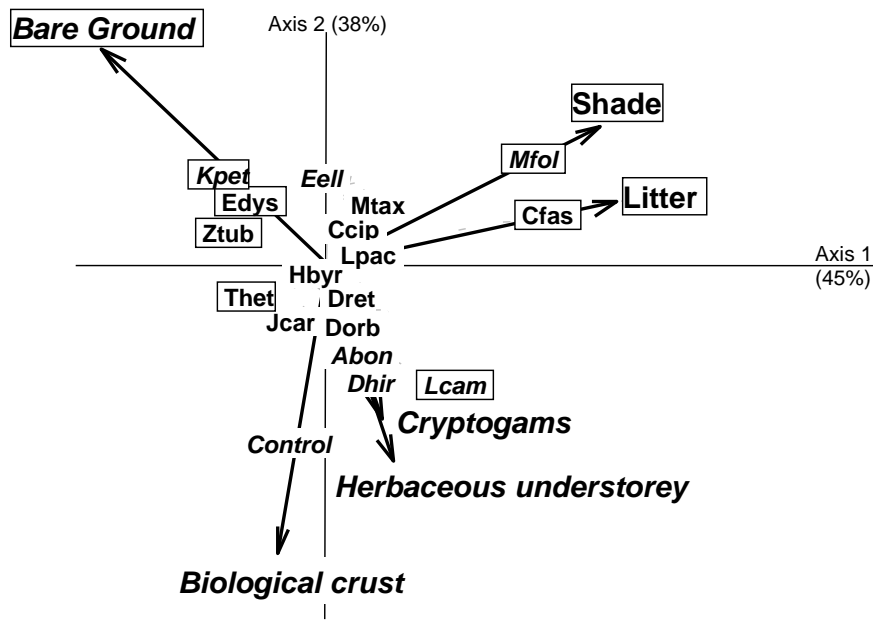


691

692 **Figure 1:** sketch of the experimental design: two sites were assigned to shrub transplantation. In each site, 30 4-
 693 m² plots were defined and two plots were randomly assigned to each shrub species (14 species x 2 plots); only
 694 two 4-m² plots remained unplanted as controls for the study of species influence on soil surface indicators.

695 Because of the small size of both sites, we could not place 28 control plots with nothing planted on them, as it
 696 would be an ideal scenario. One site was assigned to tree transplantation, sixteen 16-m² plots were assigned for
 697 tree species plantation (4 species x 4 plots). In each plot, 16 individuals of one species were transplanted 1m
 698 apart for tree species and 0.5m apart for shrub species.

699



700

701 **Figure 2:** Inter-class PCA carried out on various soil surface indicators and shade, projection of two first
 702 principal components [72 points \times 6 variables]. Variables and species contributing to axis 1 are framed and to
 703 axis 2 are in italics. Monte-Carlo permutations: inertia = 0.35, $P < 0.01$. *Chamaecrista semaphora* was not
 704 included in the analysis. Abbreviations refer to Table 1.

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