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5 Evaluation of window flight traps for effectiveness at monitoring dead wood  
6 associated beetles: the effect of ethanol lure under contrasting environmental  
7 conditions

8

9

10 Running title: Baited window flight traps and saproxylic beetles

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26 **Keywords** : optimization, sampling methods, efficiency, monitoring, alcohol bait

27

28 **Abstract**

29 1. Since the species-rich group of saproxylic beetles has been proposed to be used as  
30 a factor in forest management, more explicit knowledge about the efficiency and  
31 selective properties of beetle sampling methods is needed.

32 2. We compared saproxylic beetle assemblages caught by alcohol-baited or unbaited  
33 window traps in different forest contexts. Considering that trap attractiveness  
34 depends on kairomone concentrations, we appraised whether the trap efficiency was  
35 influenced by trap environment (openness and local supply of fresh dead wood).

36 3. Saproxylic beetles were sampled using 48 cross-vane window flight traps,  
37 arranged in paired designs (alcohol-baited/unbaited), in 8 ancient and 8 recent gaps  
38 (open stands), and 8 closed-canopy control stands in an upland beech forest in the  
39 French Pyrenees.

40 4. Baited traps were more efficient than unbaited devices in terms of abundance and  
41 richness in our deciduous forests. The ethanol lure did not have any repellent effect  
42 on the individual response of saproxylic taxa.

43 5. The influence of local environmental conditions on trap attractiveness was  
44 observed. The effects of variations in openness were actually moderate, whereas trap  
45 attractiveness appeared to be reduced in the alcohol-saturated environment of recent  
46 gaps due to a disruption by local fresh dead-wood concentrations of the kairomonal  
47 response of saproxylic beetles to baited traps ('alcohol disruption').

48 6. Since the ethanol lure globally enhances species detection probability (no repellent  
49 effect, many individual attractive effects), it may be extensively used in programs of  
50 early-warning surveillance, monitoring and control of wood borers. We recommend  
51 to account for the slight influences of local conditions on baited trap efficiency while  
52 using them for beetle biodiversity monitoring.

53 Introduction

54 Forest management practices currently include many nature conservation measures  
55 in favour of fauna and flora. Nonetheless, in managed forest ecosystems, the dead  
56 wood component has been severely reduced by intensive forestry and still is under-  
57 represented (Siitonen, 2001).

58 Since considerable effort is devoted to preserving dead wood and the associated  
59 fungi and fauna involved in the wood decaying process, we need an explicit  
60 ecological assessment of the performance of forestry measures designed to increase  
61 deadwood.

62 Saproxylic beetles have been widely studied over the past 20 years, especially in  
63 northern and central Europe, and have been proposed as indicator species of forest  
64 integrity (Speight, 1989 ; Nilsson et al., 2001) because they are highly dependent on  
65 dead wood and have been particularly affected by forest management practices (e.g.  
66 Siitonen, 2001 and references therein). They make up one of the largest groups of  
67 red-listed species, and they represent many different functional groups (Siitonen,  
68 2001).

69 As saproxylic beetles are diverse, and mainly small and cryptic, their study is very  
70 challenging. If we want to use saproxylic beetles as a management tool in forestry  
71 (evaluation of practices, biodiversity monitoring schemes), we need much more  
72 explicit knowledge about the efficiency and selective properties of sampling  
73 methods.

74

75 Several different methods are generally used to collect saproxylic beetles. These are  
76 (i) direct active hand-collecting techniques, including peeling, sifting the bark of  
77 dead trees and beating dead wood, (ii) rearing techniques (log emergence traps,

78 Owen traps, ecollectors, extraction cylinders) and (iii) trapping methods such as  
79 interception or attractive (coloured, silhouette, chemo-attractive) traps (Leather,  
80 2005). Window-flight trapping (WFT), also called Flight-Intercept Trapping (FIT),  
81 window/ barrier trapping or collision trapping), developed by Chapman & Kinghorn  
82 Peck & Davies, 1980), is currently the most frequently used technique for catching  
83 active flying saproxylic beetles (Økland, 1996 ; Wikars et al., 2005 ; Alinvi et al.,  
84 2007). Window flight traps consist of a vertical barrier to insect flight that is  
85 considered invisible to the insect. On hitting the barrier, most beetles drop down and  
86 fall into a collection container with liquid preservatives.

87 Although interception traps do not give accurate information about the local habitat,  
88 they have proved to be satisfactory in many respects. Compared with extraction  
89 methods they offer reliable means of replication and standardization, and give a  
90 representative picture of saproxylic beetle fauna (Siitonen, 1994).

91

92 From the original simple model of flight-interception trap, modifications have been  
93 proposed concerning the dimensions, colour, shape, bait... For instance, window-  
94 flight traps may be fitted with an attractant dispenser to increase catches of dead  
95 wood associated beetles (Brustel, 2004).

96 Dead wood associated species have evolved behavioral responses to volatile host-  
97 plant chemicals that indicate the presence of a suitable host (i.e. kairomones). It is  
98 well known that ethanol, a volatile compound released by micro-organisms in  
99 decaying woody tissue (mainly in fresh tissues ; Cade et al., 1970) and stressed  
100 plants (Kimmerer & Kozlowski, 1982), acts as a foraging kairomone (used in the  
101 context of food location ; Döring, 1955; Ruther et al., 2002). It is therefore attractive  
102 to a wide variety of species of dead wood associated beetles (Montgomery & Wargo,

103 1983 ; Lindelöw et al., 1992), including early- (Nordlander et al., 1986 ; Byers,  
104 1989) and late-successional saproxylic species (Jonsell et al., 2003), and beetles  
105 associated with dead wood from deciduous (Roling & Kearby, 1975) or conifer trees  
106 (Magema et al., 1982 ; Chénier & Philogène, 1989).

107 Previous studies have already demonstrated the general effects of ethanol as a lure in  
108 attractive window flight traps (Berti & Flechtmann, 1986; Shibata et al., 1996). In  
109 this study comparing two sampling techniques in paired designs, we first intended to  
110 confirm and detail the differences in catches between alcohol-baited and unbaited  
111 traps under field conditions.

112 Secondly, we wanted to assess whether the catches of dead wood associated beetles  
113 in alcohol-baited or unbaited traps are influenced by local environmental conditions.  
114 Indeed, we need standardized unbiased methods to study the effects of forest  
115 management practices and compare open (e.g. felling areas) and closed-canopy  
116 stands; ideally saproxylic beetle detectability should not change with habitat  
117 structure. We thus asked the two following questions.

118 (i) Did the difference between the two methods (alcohol-baited and unbaited traps)  
119 remain constant in open gaps or closed-canopy stands? From Schroeder and  
120 Lindelöw (1989), release rates of chemicals are known to affect the attraction. We  
121 may assume that kairomone volatility, and therefore trap attractiveness, increases  
122 with stand openness. In this perspective, the difference between baited and unbaited  
123 traps would be expected to be higher in open areas than in closed-canopy stands.  
124 This bias variation between stands would call into question the between-stand  
125 comparison using alcohol-baited traps.

126



127 (ii) Did the difference between the two methods remain constant whether or not the  
128 close trap surroundings were poor or rich in naturally emitted ethanol from fresh or  
129 decaying dead wood?

130 We may assume that trap attractiveness is influenced by the alcohol concentration in  
131 the atmosphere surrounding the trap. In recent sun-exposed gaps, the high volumes  
132 of fresh dead wood release a large amount of ethanol, which may lead to a saturated  
133 olfactory landscape and therefore to a reduction in the capture efficiency of the trap  
134 attractant. Due to an alcohol disruption, we hypothesize that the differences between  
135 paired baited and unbaited traps would be lower in recent gaps than in both old gaps  
136 and forest controls where the local atmosphere is not alcohol-saturated.

137

## 138 **Material and methods**

### 139 **Study areas and sampling designs**

140 Our investigations were carried out in an upland beech forest in the central French  
141 Pyrenees, in the National Orlu Reserve, about 150 km south of Toulouse. Altitude  
142 ranged from 1600 m to 1750 m. The selected plots were 100 to 140 year-old beech  
143 stands, and had previously been exploited for charcoal by coppicing.

144 The balanced sampling design included three types of stands: 8 ancient gaps, 8 recent  
145 gaps (open stands) and 8 forest controls (closed-canopy stands). The 16 gaps were  
146 originally dedicated to the monitoring of conservation measures in favour of the  
147 Western capercaillie (*Tetrao urogallus*, L. 1758). Ancient and recent gaps were  
148 created in 1999 and 2004 respectively; they were circular in shape and ca 0.05 ha in  
149 area. Distance between gaps varied from 80 m to 1000 m. Cut trees were left in all  
150 gaps but only recent gaps had high amounts of recent (freshly-cut) dead wood. In  
151 parallel, a transect of 8 forest control plots was set up in closed-canopy beech stands,

152 where the cover was quite dense (basal area = 23 m<sup>2</sup>/ha, stem density = 300 stems/ha,  
153 mean dbh = 25cm, mean height=15m) and the understory very poor.

#### 154 **Beetle sampling**

155 Beetles were sampled with a multidirectional Polytrap<sup>TM</sup> (Brustel, 2004), a cross-  
156 vane window flight trap with a cumulative panel area of 1 m<sup>2</sup> ((Fig. 1). For the

Fig. 1

157 preservation of insects, containers were half-filled with a salt mixture. A detergent  
158 was added to reduce surface tension. Two traps were set in each plot, one baited with  
159 an alcohol lure (1:10 ethanol released from a dispenser) and one unbaited trap.  
160 Alcohol lure is known to attract hardwood-feeding species (Mongomery & Wargo,  
161 1983).

162 Overall, 24 pairs of Polytraps<sup>TM</sup> were set up in 2004, from May 15 to August 30 in  
163 recent and ancient gaps and closed-canopy beech stands. The traps were emptied  
164 every two weeks.

165 Collected specimens were stored in alcohol and we identified them to species level.  
166 Several amateur entomologists helped with the identification on the following  
167 families: Anobiidae, Curculionidae, Dasytidae, Melyridae, Mordellidae, Pselaphidae,  
168 Scolytinae, Scaptiidae, Staphylinidae. The nomenclature follows the online  
169 FaunaEuropaea database ([www.faunaeur.org](http://www.faunaeur.org)). We pooled the data for the entire  
170 sampling period.

171

#### 172 **Data processing**

173 The two sampling methods were compared in terms of total saproxylic beetle  
174 abundance, cumulative species number per trap, family and species abundance per  
175 trap (cumulated over the trapping periods).

176 Linear mixed-model ANOVA tests (Pinheiro & Bates, 2000) were carried out to  
177 check for differences in abundance and species richness between the two trap types  
178 in each paired comparison. The plot variable was classified as a spatial random effect  
179 to take the pairing pattern of the sampling design into account. Some differences  
180 were exceptionally tested by Wilcoxon signed-rank tests. Species and families  
181 represented by fewer than 30 individuals were not tested.

182 The effects of the interaction between bait and two factors on total abundance and  
183 abundance of alcohol-attracted taxa (in our data), species richness were assessed. The  
184 three stand types of the study were clustered using two different grouping factors.  
185 First, to study the influence of stand openness on trap attractiveness, we compared  
186 the difference between paired baited and unbaited traps in open (recent and ancient  
187 gaps) or closed-canopy stands. We analysed this difference through the interaction  
188 effect in linear mixed-model ANOVAs (bait\*openness). Second, to study the  
189 influence of local fresh dead wood concentrations on trap attractiveness, we  
190 examined the difference (baited - unbaited) in fresh dead-wood rich (recent gaps) or  
191 poor (ancient gaps and forest controls) stands. The F-test of the interaction effect  
192 (bait\*stand type) in linear mixed-model ANOVAs was followed by a multiple  
193 comparison post hoc Tukey test of the mean value of this difference.

194 Graphs include multipanel boxplots displaying the distribution of data according to  
195 the two factors bait\*environment, or simple boxplots showing the numerical  
196 difference (baited-unbaited) for different environment types.

197 Non-Metric Multidimensional Scaling (NMDS) based on the Bray-Curtis  
198 dissimilarity was used for pattern recognition in species composition and the  
199 ANOSIM procedure was carried out to test for differences in assemblage  
200 composition between trap types (Clarke, 1993). Before calculation of the Bray-Curtis

201 distance matrix, species represented by only 1 individual were discarded and  
202 abundance data were (ln+1) transformed.

203 ANOVA, NMDS and ANOSIM were performed using S.Plus 7.0.

204

## 205 **RESULTS**

206 When baited with alcohol, window flight traps were more selective: the ratio  
207 (number of saproxylic beetles/number of beetles) reached 85.8% in baited traps but  
208 was only 69.4% in unbaited traps. A total of 12,211 saproxylic beetles were  
209 identified during the study, including 196 species.

210

### 211 **Comparison of effectiveness between alcohol-baited and unbaited traps**

212 Alcohol-baited or unbaited traps significantly differed in effectiveness. The catches  
213 of saproxylic beetles were significantly affected by the alcohol lure (mixed-model  
214 ANOVA  $F_{(1,23)}= 66.48$ ,  $p<0.0001$ ; Table 1). Overall, more than twice as many  
215 saproxylic beetle individuals were captured in alcohol-baited traps as in unbaited  
216 traps (Table 1).

#### **Tab. 1**

Similarly, significantly more saproxylic species were caught in alcohol-lured traps  
218 than in unbaited (ANOVA  $F_{(1,23)}= 68.65$ ,  $p<.0001$  ; Table 1). The richness per trap

#### **Fig. 2**

219 was 40% higher in baited traps than in unbaited traps (Table 1). From the ordination  
220 plot of the Bray-Curtis distance matrix between samples (Fig. 2), the species  
221 composition of saproxylic beetle assemblages caught with or without an alcohol lure  
222 clearly differed. Samples from baited or unbaited traps were obviously separated in  
223 ordination space. This distinction was consistent with the results of the ANOSIM test  
224 (10 000 permutations,  $R=0.65$ ,  $p<0.0001$ ). The average Bray-Curtis dissimilarity  
225 between baited and unbaited traps reached a value of 44%.

226 In accordance with this global dissimilarity, important specific differences were  
227 noticed. For several families and species (Cryptophagidae (*Cryptophagus* spp.),  
228 Staphylinidae (*Paraphloeostiba gayndahensis*, *Aleochara sparsa*), Salpingidae  
229 (*Rhinosimus ruficollis*, *R. planirostris*, *Rabocerus foveolatus*)), significantly more  
230 individuals were caught in baited traps than in unbaited traps (mixed-model  
231 ANOVA; Table 2). *Rhizophagus* spp. (Monotomidae) was more abundant in baited  
232 traps compared with unbaited traps, whereas Cleridae were not affected by trap bait.  
233 Amongst xylophagous taxa, Scolytidae (*Ernoporicus fagi*, *Xyloterus signatus*, *X.*  
234 *domesticus*, *Xyleborus saxesenii*) and Lymexylidae (*Hylecoetus dermestoides*) were  
235 more abundantly caught in baited traps, whereas Cerambycidae, Anobiidae,  
236 Melyridae were not sensitive to alcohol bait.

**Tab. 2**

No species or family was significantly more abundant in unbaited traps.

238

239 **Comparison of effectiveness between alcohol-baited and unbaited traps in open**  
240 **or closed-canopy stands**

241 The difference between alcohol-baited and unbaited traps in open (gaps) or closed-  
242 canopy stands may be interpreted first in terms of abundance or species richness. As

**Fig. 3**

shown in figure 3, saproxylic beetle abundance in both baited and unbaited traps was  
244 higher in open sites than in closed-canopy controls. The difference in abundance  
245 between baited and unbaited devices was only slightly higher in open plots; in other  
246 words, the bait-openness interaction effect was quite moderate (mixed-model  
247 ANOVA test  $F_{2,21} = 5.17$ ,  $p = 0.015$ ).

248 The difference in species richness between baited and unbaited traps was not  
249 significantly influenced by the openness of trap environment (Fig. 3: mixed-model  
250 ANOVA test of the bait-openness interaction effect:  $F_{2,21} = 3.23$ ,  $p = 0.060$ ).

251

252 For several taxa noticed to be sensitive to the alcohol attractant (see above), i.e.  
253 Monotomidae, Scolytidae and Lymexylidae as a whole, the difference baited-  
254 unbaited was not affected by the environment closure. Two families  
255 (Cryptophagidae, i.e. *Cryptophagus* spp., and Salpingidae), and 4 species (*Rabocerus*  
256 *foveolatus*, *Rhinosimus ruficollis*, *Rhinosimus planirostris*, *Aleochara sparsa*)  
257 showed a significant difference baited-unbaited, but not in compliance with the  
258 hypothesis of a bait-openness interaction. The difference was indeed lower in open  
259 stands than in closed-canopy plots (fig. 4). Only the bark beetle species *Xyloterus*  
260 *domesticus* showed a significant and higher difference baited-unbaited in open  
261 stands.

Fig. 4

262 In conclusion, the difference between alcohol-baited and unbaited traps was not  
263 increased greatly by the openness of trap environment.

264

#### 265 **Comparison of effectiveness between alcohol-baited and unbaited traps in fresh** 266 **dead wood poor or rich stands**

267 Regarding this potential bait-environment interaction effect, the difference between  
268 alcohol-baited and unbaited traps was only slightly influenced by the local volume of  
269 fresh woody debris releasing alcohol kairomones. The baited-unbaited difference in  
270 fresh dead wood poor (ancient gaps and controls) or rich stands (recent gaps) was  
271 examined in terms of total abundance, species richness, family and species  
272 abundances.

273 In figure 5, the difference between baited and unbaited lures in terms of abundance  
274 and species richness seems to be slightly lower in gaps rich in recent fresh dead  
275 wood. Nevertheless, this bait-environment interaction effect was only slightly

Fig. 5

276 significant on saproxylic beetle abundance (mixed-model ANOVA,  $F_{2,35} = 4.84$ ,  $p =$   
277 0.014). The only significant pairwise difference was observed between ancient and  
278 recent gaps (Multiple comparison Tukey test), the difference being larger in ancient  
279 gaps. This bait-environment interaction did not significantly affect species richness  
280 in traps (mixed-model ANOVA,  $F_{2,35} = 1.66$ ,  $p = 0.204$ ).

**Fig. 6**

281 A bait-environment interaction effect was observed on the abundance of several  
282 families and species known to be sensitive to the ethanol attractant (fig. 6). The  
283 baited-unbaited differences were lower in recent gaps than in ancient gaps and forest  
284 controls for the abundance of Salpingidae (and the species *Rhinosimus ruficollis* in  
285 particular) (multiple comparison Tukey test). Similarly, we observed a smaller yet  
286 still significant baited-unbaited difference for the abundance of Cryptophagidae and  
287 *Rhinosimus planirostris* in recent gaps compared with closed-canopy stands. For  
288 *Rabocerus foveolatus*, *Aleochara sparsa*, *Xyloterus signatus*, the difference was less  
289 in recent gaps than in closed-canopy controls (but the difference between ancient or  
290 recent gaps was not significant). No difference was measured for Scolytidae as a  
291 whole (and *Xyloterus domesticus*, *Ernoporicus caucasicus*, *Xyleborus saxesenii* in  
292 particular), Lymexylonidae, Staphylinidae (peculiarly *Paraphloeostiba gayndahense*)  
293 and Monotomidae (*Rhizophagus* spp. in particular).

294

295 Discussion

296

297 Alcohol lure effect

298 The results from our study confirm that ethyl alcohol, acting as a kairomone released  
299 from decaying woody tissues, strongly attracts some beetles associated with dead  
300 hardwood (Montgomery & Wargo, 1983) and suggests that an ethanol lure

301 strengthens the effectiveness of window-flight traps in deciduous forests. Indeed,  
302 more than twice as many saproxylic beetles, representing a 40% higher species  
303 richness, were captured in alcohol-baited traps as in unbaited traps. Assemblages  
304 were globally dissimilar between baited and unbaited devices, mainly because more  
305 species were caught in baited traps. It is very important to stress that we did not  
306 detect any species or family significantly more abundant in unbaited traps. We may  
307 therefore infer that the ethanol lure did not have any inhibiting or repellent effect.

308

309 In our methodological approach in beech forests, the individual responses of dead-  
310 wood taxa to alcohol lure were actually heterogeneous. As previously demonstrated  
311 by Byers (1992), significantly more individuals of *Rhizophagus* spp. (Monotomidae)  
312 were caught in baited traps than in unbaited traps. Host tree chemicals are known to  
313 be important to *Rhizophagus* species in finding their habitat (scolytid galleries).  
314 Conversely, natural enemies such as Cleridae were not affected by trap bait in our  
315 study. Likewise, Schroeder (2003) pointed out that two *Thanasimus* clerid species  
316 preying on several bark beetle species differ in their response to  $\alpha$ -pinene and  
317 ethanol. Our results showed that the abundance of ambrosia and bark beetles was  
318 about 4 times as high in alcohol-baited traps, in agreement with previous findings  
319 (Magama et al., 1982 ; Berti & Flechtmann, 1986 ; Poland et al. 2004). Amongst the  
320 other wood-feeding taxa, Cerambycidae were not sensitive to alcohol bait, which had  
321 been shown previously by Sweeney et al. (2004). Conversely, Döring (1955)  
322 demonstrated that ethanol acts as a kairomone for the longhorned beetle *Cerambyx*  
323 *cerdo*. Among the fungus feeders, unlike Tetratomidae, Melandryidae and Ciidae,  
324 only Cryptophagidae were significantly attracted by the alcohol lure, as was the  
325 tenebrionid studied by Jonsell et al. (2003).



326

327 Interaction effects between trap attractant and trap environment

328 Some results did not comply with the hypothesized bait-openness interaction. Five  
329 species showed a significant lower baited-unbaited difference in open areas.  
330 Moreover, the baited-unbaited difference in species richness and in abundance of the  
331 other alcohol-attracted taxa was not significantly influenced by the openness of trap  
332 environment. Only the total saproxylic beetle abundance and the abundance of the  
333 bark beetle *Xyloterus domesticus* were in accordance with the hypothesis of an  
334 increased baited-unbaited difference in open areas compared with closed-canopy  
335 stands. In other words, trap attractiveness appeared to increase only slightly, but not  
336 significantly, with stand openness, even though canopy cover may strongly influence  
337 kairomone volatility. However, such an interaction effect was reported by Honek  
338 (1988), between crop density and an attractant in pitfall traps, on catches of epigeic  
339 arthropods.

340

341 Apart from openness, another environmental factor separated the plots into groups.  
342 Indeed, recent gaps, ancient gaps and forest controls differed in terms of local  
343 volume of fresh dead wood. We hypothesized that the high volume of fresh dead  
344 wood in recent sun-exposed gaps would release a large amount of ethanol, which  
345 could saturate the beetle's olfactory landscape around the traps and therefore reduce  
346 trap attractiveness. In accordance with this hypothesis, the baited-unbaited difference  
347 was lower in recent and fresh dead wood rich gaps for some assemblage parameters.  
348 Though this bait-environment interaction was slight, it significantly affected the total  
349 abundance of saproxylic beetles, the abundance of several families and species  
350 known to be sensitive to the ethanol attractant (Salpingidae, *Rhinosimus ruficollis*

351 and *Rhinosimus planirostris* in particular, Cryptophagidae). Conversely, the response  
352 of species richness and abundance of the other families (such as Scolytidae) to traps  
353 was not influenced by the local volume of fresh dead wood.

354 The alternative hypothesis of a “mass effect”, i.e. a stronger attractiveness of baited  
355 traps in the alcohol-rich atmosphere of recent gaps, was thus invalidated. These  
356 results may be related to a phenomenon that could be called ‘alcohol disruption’ (in  
357 the spirit of the ‘mating disruption’; Ruther et al., 2002), i.e. the disruption by local  
358 fresh dead-wood concentrations of the kairomonal response of saproxylic beetles to  
359 baited traps. Nonetheless, even though trap attractiveness appeared to be reduced in  
360 an alcohol-saturated environment, baited traps remain more efficient than unbaited  
361 devices in terms of abundances and richness. They have the capacity to sample the  
362 pool of saproxylic beetles in recent gaps.

363

#### 364 **Conclusion - Implications for saproxylic beetle sampling**

365 Even though the extrapolation of our findings from upland forests to other climatic  
366 contexts should be done with care, their interpretation may help with the  
367 optimization of the two types of forest beetle monitoring.

368 The first type, i.e. monitoring and control of forest pest populations and early-  
369 warning surveillance programs to detect invasive wood borers, aim at maximizing  
370 detection probability. We demonstrated that the ethanol lure does not have any  
371 repellent effect but significantly attracts several wood feeders. Like the New Zealand  
372 monitoring programme for invasive wood-feeders (Brockerhoff et al., 2006),  
373 effective sampling designs may use the large spectrum of ethanol attractiveness.

374 The second type, i.e. biodiversity surveys of saproxylic beetle diversity in monitoring  
375 networks or evaluation studies of forest management practices, implies distinct

376 constraints. To compare the biodiversity between stands or to assess trends in  
377 saproxylic beetle diversity over broader landscapes, ideally saproxylic beetle  
378 detectability should not change with habitat structure. A variation in trap efficiency  
379 as a function of any stand environmental parameter would call into question an inter-  
380 site comparison. For instance, a relation between trap efficacy and stand openness  
381 would prevent the comparison of open (e.g. felling areas) and closed-canopy stands  
382 with alcohol-baited traps, or studies on the influence of shading for the attractiveness  
383 of dead wood (Hjältèn et al., 2007). Our results show slight interaction effects  
384 between trap attractant and trap environment. A very moderate bait-openness  
385 interaction effect was measured, whereas trap attractiveness appeared to be reduced  
386 in an alcohol-saturated environment, through a disruption by local fresh dead-wood  
387 concentrations of the kairomonal response of saproxylic beetles to baited traps  
388 ('alcohol disruption').

389 In accordance with these results and although alcohol-baited traps appeared to be  
390 more efficient than unbaited devices, we recommend to take care to use baited  
391 brine or glycol solution used as a preservative fluid does not vary with forest stands.  
392 Beside the attractant, other trap parameters, such as colour and shape, should be  
393 assessed for optimization and standardization and have been partly examined in  
394 another study (Bouget et al., in press).

395 Acknowledgements

396

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404

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510

511 Figure legends

512

513 Figure 1

514 Design of the cross-vane window flight trap used during the study

515

516 Figure 2

517 NMDS ordination plot of the Bray-Curtis dissimilarity matrix of baited (AL) and  
518 unbaited (NAL) samples. The two axes with highest correlation to bait factor are  
519 represented. 4-dimension stress = 0.153. ANOSIM test (10 000 permutations)  
520 confirmed the difference of assemblages ( $R=0.65$ ,  $p<0.0001$ ).

521

522 Figure 3

523 Mean abundance (a) and species richness (b) per trap of saproxylic beetles in baited  
524 (AL) and unbaited (NAL) traps in open (MO) or closed-canopy (MF) stands. Linear  
525 mixed-model ANOVA F-test significance of the interaction effect between bait and  
526 openness: \*\*  $p<0.01$ , \*  $0.01<p<0.05$ , ns  $p>0.05$ .

527

528 Figure 4

529 Mean difference in abundance per trap of saproxylic beetle families (a) and species  
530 (b) between baited (AL) and unbaited (NAL) traps in open (MO) or closed-canopy  
531 (MF) stands. Mann-Whitney test significance: \*\*  $p<0.01$ , \*  $0.01<p<0.05$ , ns  $p>0.05$ .  
532 Only species and families including more than 30 individuals were tested.

533

534 Figure 5

535 Mean species richness (a) and abundance (b) per trap of saproxylic beetles in baited  
536 (AL) and unbaited (NAL) traps in fresh dead wood poor stands [forest controls (F)  
537 and ancient gaps (TA)] and fresh dead wood rich stands [recent gaps (TR)]. Linear  
538 mixed-model ANOVA test significance: \*\*  $p < 0.01$ , \*  $0.01 < p < 0.05$ , ns  $p > 0.05$ .

539 Mean difference in richness (c) and abundance (d) between baited and unbaited traps  
540 in fresh dead wood poor stands [F, TA] and fresh dead wood rich stands [TR].  
541 Different letters indicate significant differences between means after a post-hoc  
542 Tukey test ( $p = 0.01$ ).

543

544 Figure 6

545 Mean difference in abundance per trap of saproxylic beetle families (a) and species  
546 or genera (b) between baited and unbaited traps in fresh dead wood poor stands  
547 [forest controls (F) and ancient gaps (TA)] and fresh dead wood rich stands [recent  
548 gaps (TR)]. Linear mixed-model ANOVA test significance: \*\*  $p < 0.01$ , \*  
549  $0.01 < p < 0.05$ , ns  $p > 0.05$ . Different letters indicate significant differences between  
550 means after a post-hoc Tukey test ( $p = 0.01$ ). Only species and families including  
551 more than 30 individuals were tested.

552

553 Tables

554

555 Table 1

556

557 Differences between baited (AL) and unbaited (NAL) traps, in terms of saproxylic  
558 beetle abundance, species richness. Test significance: \*\*  $p < 0.01$ , \*  $0.01 < p < 0.05$ , ns  
559  $p > 0.05$ . Differences were tested by linear mixed-model ANOVA F-tests. Mean  
560 values are expressed +/- Standard Deviation.

561

Taxa	Alcohol-baited traps	Unbaited traps	
Abundance	331,417 +/- 156,330	143,750 +/- 55,155	$F_{(1,23)}=66,482$ **
Species richness	43,125 +/- 9,768	31,458 +/- 8,827	$F_{(1,23)}=68,649$ **

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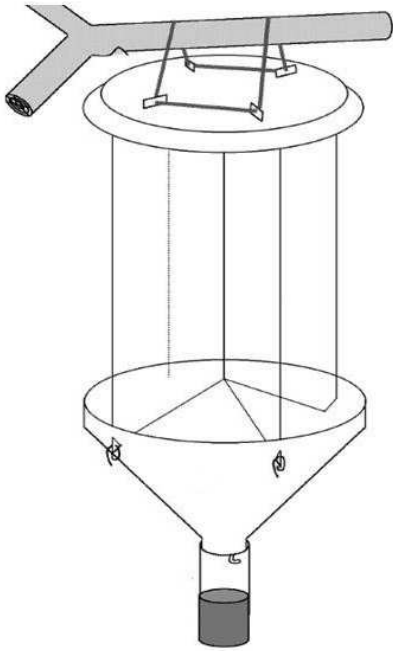
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Table 2

Mean abundance per trap of saproxylic beetle species and families in baited (AL) and unbaited (NAL) traps. Linear mixed-model ANOVA test significance: \*\* p<0.01, \* 0.01<p<0.05, ns p>0.05. Mean values are expressed +/- Standard Deviation.

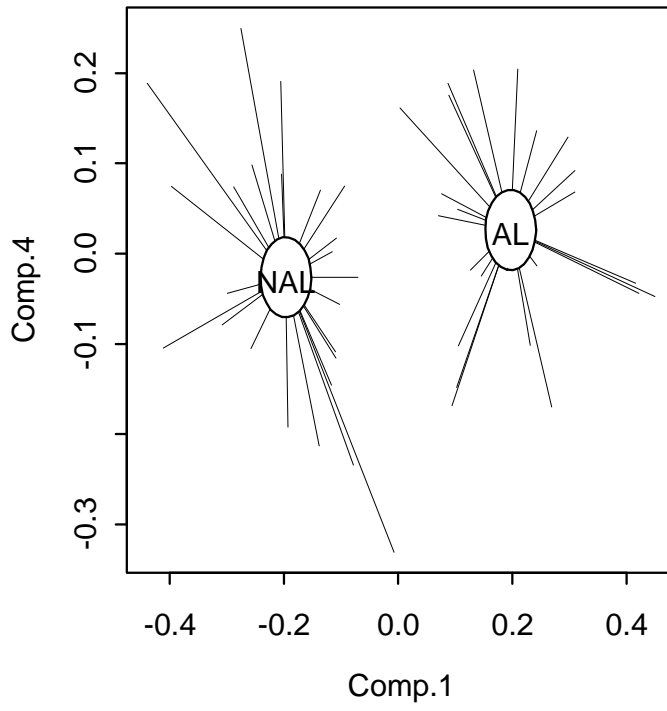
Taxa	Alcohol-baited traps	Unbaited traps	F <sub>(1,23)</sub> p
LEIODIDAE	1,125 +/- 1,424	1,625 +/- 2,123	F=1,274 <sup>ns</sup>
STAPHYLINIDAE	49,458 +/- 28,290	34,667 +/- 19,325	F=15,243 **
<i>Aleochara sparsa</i>	1,833 +/- 1,711	0,167 +/- 0,637	F=27,688 **
<i>Eusphalerum angustum</i>	29,542 +/- 26,132	30,500 +/- 19,638	F=1,908 <sup>ns</sup>
<i>Paraphloeostiba gayndahense</i>	9,958 +/- 8,175	0,375 +/- 0,576	F=198,854 **
<i>Leptusa pulchella</i>	0,958 +/- 1,301	0,500 +/- 0,780	F=1,929 <sup>ns</sup>
LUCANIDAE	0,625 +/- 0,824	0,833 +/- 1,007	F=0,512 <sup>ns</sup>
<i>Sinodendron cylindricum</i>	0,542 +/- 0,658	0,750 +/- 0,847	F=0,682 <sup>ns</sup>
EUCNEMIDAE	1,250 +/- 2,345	0,667 +/- 1,049	F=0,414 <sup>ns</sup>
<i>Melasis buprestoides</i>	1,250 +/- 2,345	0,667 +/- 1,049	F=0,467 <sup>ns</sup>
ELATERIDAE	1,667 +/- 1,903	2,292 +/- 1,944	F=1,422 <sup>ns</sup>
<i>Idolus picipennis</i>	0,917 +/- 1,501	1,375 +/- 1,610	F=2,293 <sup>ns</sup>
ANOBIIDAE	26,500 +/- 22,043	24,042 +/- 22,160	F=0,141 <sup>ns</sup>
<i>Grynobius planus</i>	0,917 +/- 1,558	1,167 +/- 2,160	F=0,012 <sup>ns</sup>
<i>Hemicoelus costatus</i>	7,292 +/- 8,961	7,250 +/- 7,731	F=0,000 <sup>ns</sup>
<i>Ptilinus pectinicornis</i>	16,500 +/- 20,061	12,458 +/- 15,704	F=0,280 <sup>ns</sup>
<i>Ptinomorphus imperialis</i>	0,458 +/- 0,932	0,958 +/- 3,458	F=0,043 <sup>ns</sup>
<i>Xestobium plumbeum</i>	1,333 +/- 1,494	2,083 +/- 5,579	F=0,209 <sup>ns</sup>
LYMEXYLIDAE	6,333 +/- 10,639	0,375 +/- 1,279	F=38,526 **
<i>Hylecoetus dermestoides</i>	6,333 +/- 10,639	0,375 +/- 1,279	F=41,528 **
CLERIDAE	0,917 +/- 1,283	1,042 +/- 1,459	F=0,053 <sup>ns</sup>
<i>Tillus elongatus</i>	0,917 +/- 1,283	1,042 +/- 1,459	F=0,125 <sup>ns</sup>
MELYRIDAE	12,792 +/- 12,646	8,875 +/- 8,295	F=0,617 <sup>ns</sup>
MALACHIIDAE	2,000 +/- 2,537	3,292 +/- 3,196	F=3,651 <sup>ns</sup>
MONOTOMIDAE	2,417 +/- 2,263	0,250 +/- 0,442	F=60,460 **
<i>Rhizophagus spp.</i>	2,375 +/- 2,281	0,167 +/- 0,381	F=57,873 **
CRYPTOPHAGIDAE	14,625 +/- 14,984	5,917 +/- 5,823	F=17,544 **
<i>Cryptophagus spp.</i>	14,125 +/- 15,103	5,833 +/- 5,880	F=14,091 **
LATRIDIIDAE	8,625 +/- 6,851	6,000 +/- 5,703	F=3,009 <sup>ns</sup>
MYCETOPHAGIDAE	1,750 +/- 1,539	1,042 +/- 1,083	F=2,757 <sup>ns</sup>
CIIDAE	5,667 +/- 5,346	5,208 +/- 5,073	F=0,143 <sup>ns</sup>
TETRATOMIDAE	3,583 +/- 3,202	2,625 +/- 3,609	F=4,037 <sup>ns</sup>
<i>Tetratoma ancora</i>	3,583 +/- 3,202	2,625 +/- 3,609	F=4,037 <sup>ns</sup>
MELANDRYIDAE	2,250 +/- 2,592	1,542 +/- 1,615	F=1,850 <sup>ns</sup>
<i>Melandrya caraboides</i>	0,958 +/- 1,398	0,792 +/- 1,285	F=0,456 <sup>ns</sup>
MORDELLIDAE	1,333 +/- 3,199	1,083 +/- 1,909	F=0,337 <sup>ns</sup>
<i>Tomoxia bucephala</i>	0,917 +/- 2,586	0,917 +/- 1,886	F=0,316 <sup>ns</sup>
SALPINGIDAE	89,417 +/- 44,071	3,417 +/- 2,165	F=162,552 **
<i>Rabocerus foveolatus</i>	4,750 +/- 3,650	0,208 +/- 0,588	F=82,129 **
<i>Rhinosimus planirostris</i>	53,167 +/- 25,426	1,583 +/- 1,248	F=486,084 **
<i>Rhinosimus ruficollis</i>	31,458 +/- 18,967	1,583 +/- 1,472	F=201,812 **
SCRAPTIIDAE	2,292 +/- 2,510	2,458 +/- 1,719	F=1,540 <sup>ns</sup>
<i>Anaspis rufilabris</i>	1,417 +/- 1,213	1,792 +/- 1,587	F=0,428 <sup>ns</sup>
CERAMBYCIDAE	10,375 +/- 7,471	9,792 +/- 7,396	F=0,042 <sup>ns</sup>
<i>Clytus arietis</i>	1,625 +/- 2,143	1,042 +/- 1,654	F=2,878 <sup>ns</sup>
<i>Oxymirus cursor</i>	1,625 +/- 2,018	1,542 +/- 1,250	F=0,065 <sup>ns</sup>
<i>Rhagium bifasciatum</i>	3,542 +/- 3,176	3,958 +/- 3,862	F=0,007 <sup>ns</sup>
<i>Rhagium mordax</i>	1,417 +/- 1,349	1,667 +/- 2,160	F=0,005 <sup>ns</sup>
SCOLYTIDAE	81,417 +/- 127,180	22,583 +/- 21,040	F=23,698 **
<i>Ernoporicus caucasicus</i>	18,667 +/- 37,632	4,417 +/- 4,452	F=10,469 **
<i>Taphrorychus bicolor</i>	53,083 +/- 125,971	17,208 +/- 20,121	F=0,586 <sup>ns</sup>
<i>Xyleborus saxesenii</i>	4,792 +/- 3,683	0,042 +/- 0,204	F=107,812 **
<i>Xyloterus domesticus</i>	2,000 +/- 2,284	0,125 +/- 0,448	F=22,674 **
<i>Xyloterus signatus</i>	1,792 +/- 2,021	0,000 +/- 0,000	F=32,427 **

570 Figures  
571  
572 Figure 1  
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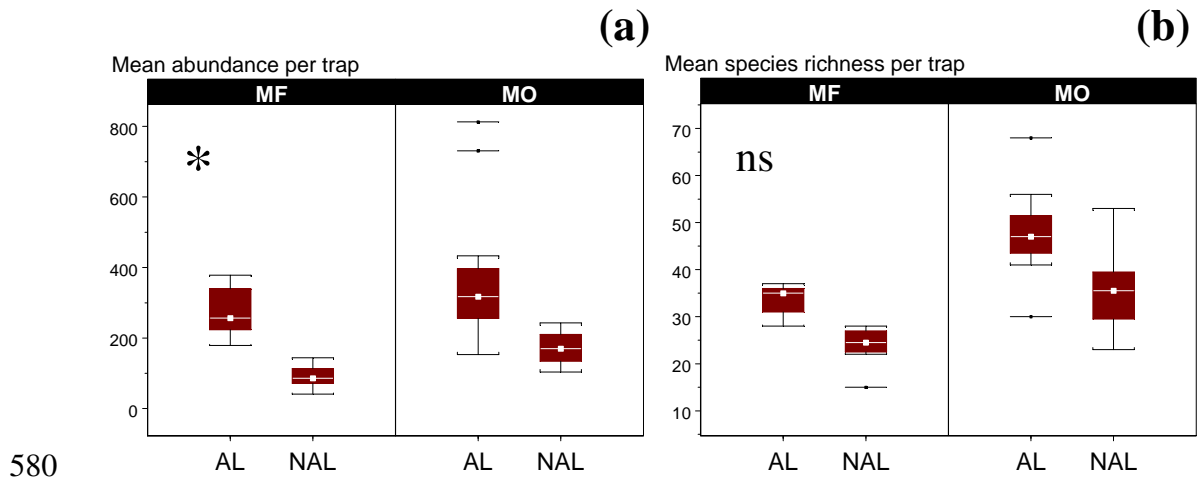


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576 Figure 2  
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578 Figure 3  
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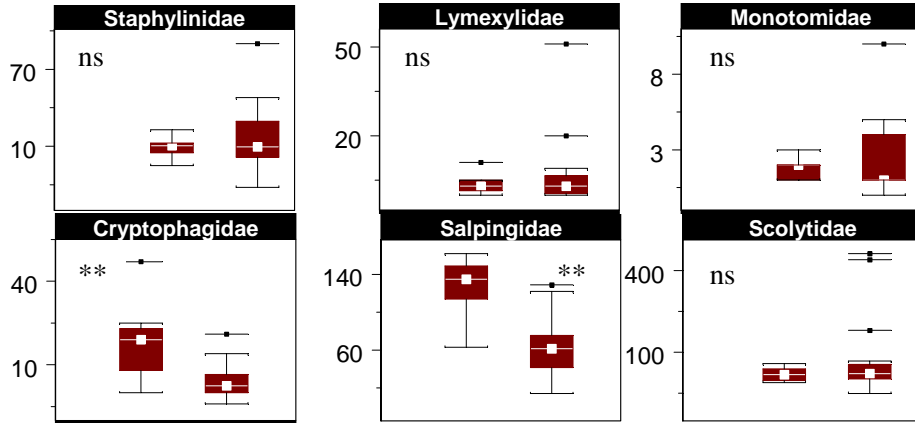


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Figure 4

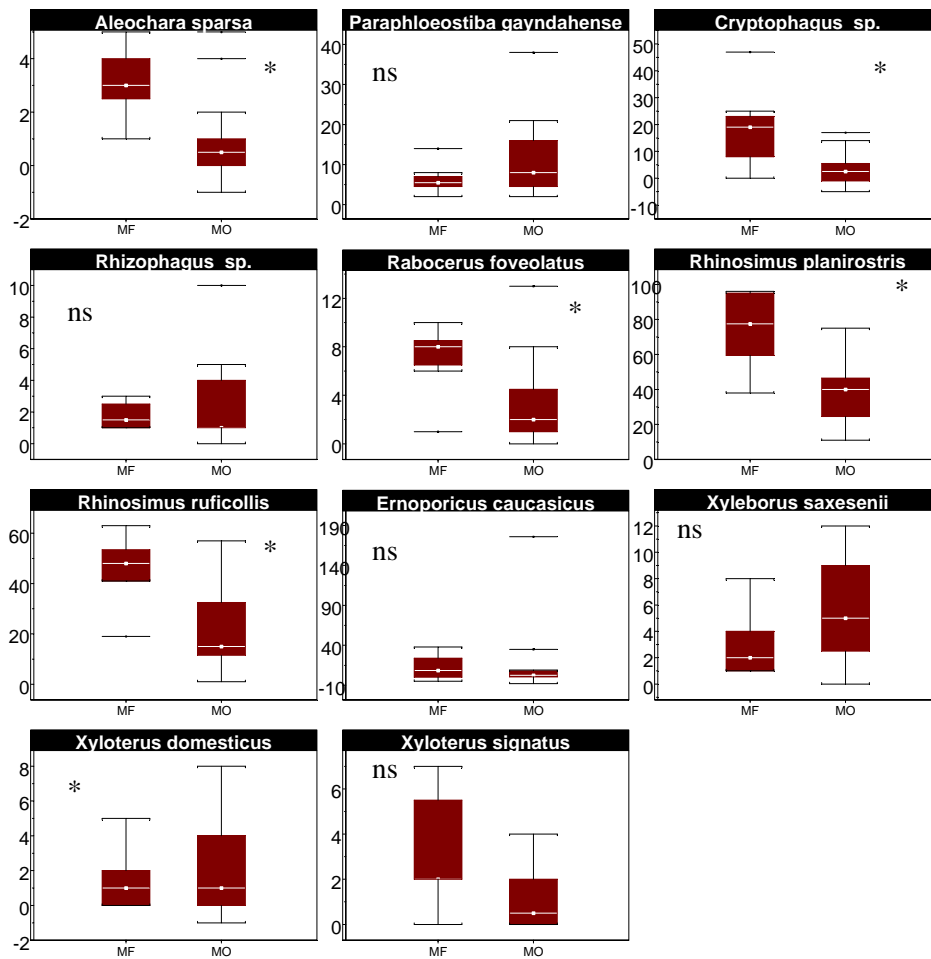
(a) Families

Difference in abundance



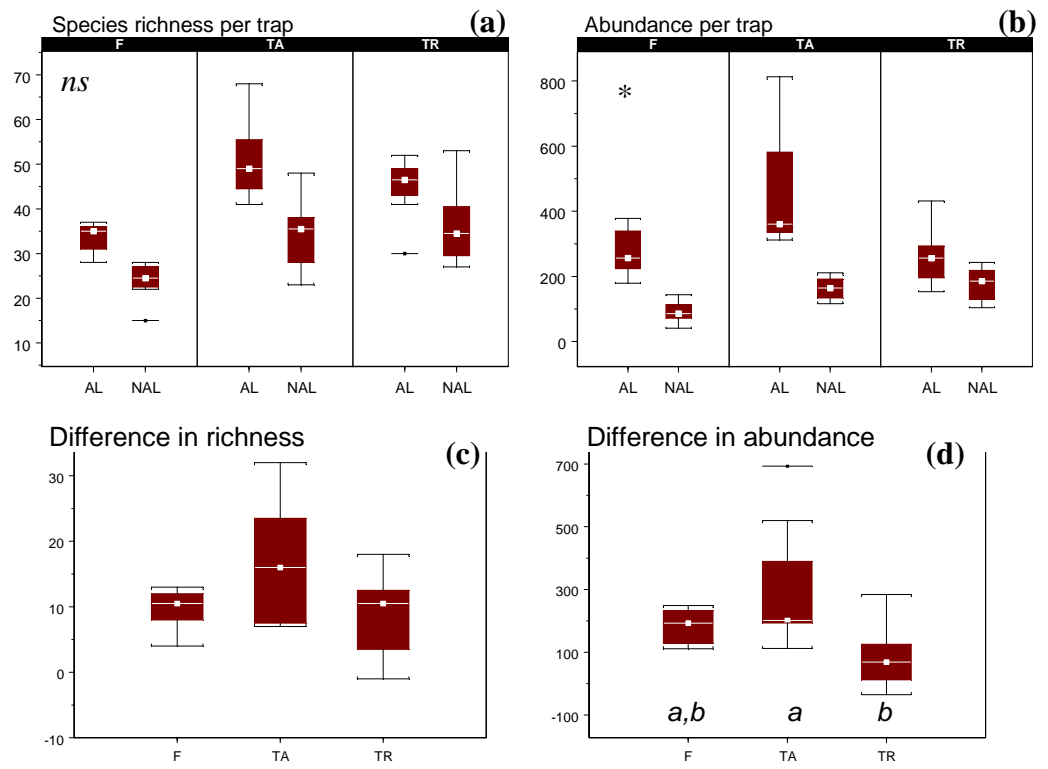
(b) Species

Difference in abundance



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587 Figure 5  
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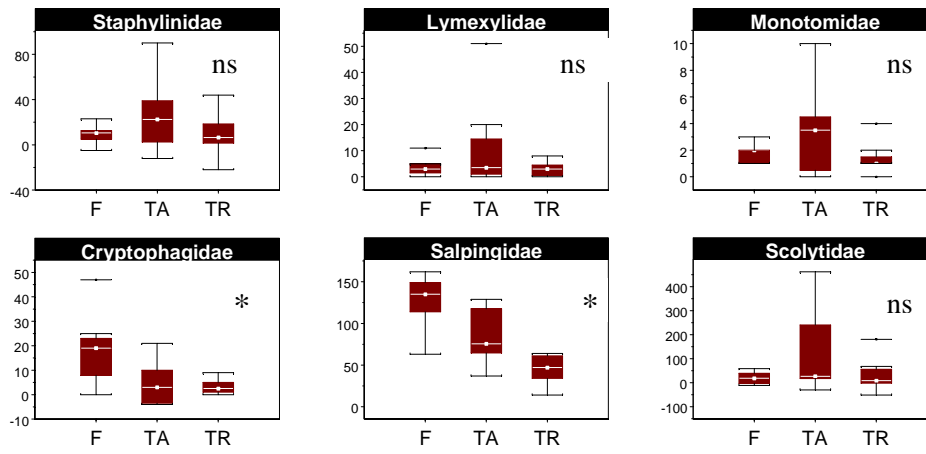
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Figure 6

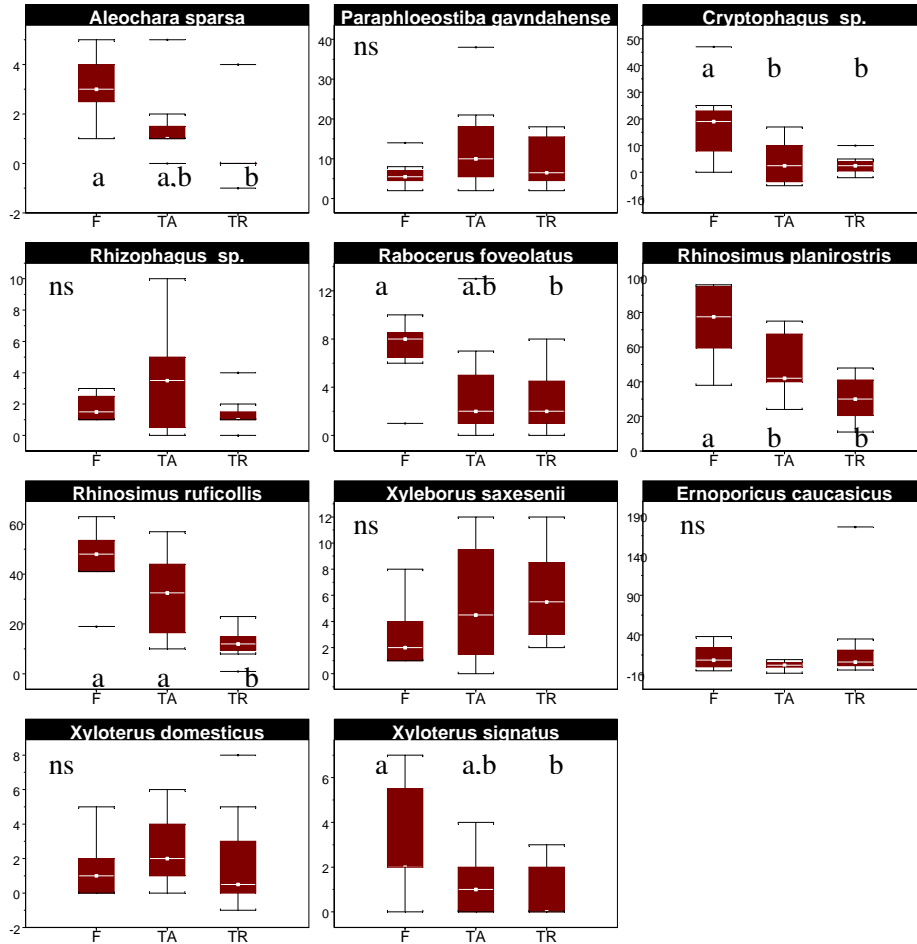
(a) Families

Differences in abundance



(b) Species

Differences in abundance



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