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Martin Faucher, Séraphine Grellier, Clémence Chaudron, Jean-Louis Janeau, Gabrielle Rudi, et al.. Mediterranean vineyard soil seed bank characterization along a slope/disturbance gradient: Opportunities for land sharing. *Agriculture, Ecosystems & Environment*, 2024, 361, pp.108821. 10.1016/j.agee.2023.108821 . hal-04300713

HAL Id: hal-04300713

<https://hal.science/hal-04300713v1>

Submitted on 22 Nov 2023

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1 Mediterranean vineyard soil seed bank characterization along a slope/disturbance
2 gradient: Opportunities for land sharing

3

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19 Abstract

20 The Mediterranean region is predicted to experience more intense rainfall events
21 separated by severe droughts due to climate change. In agrosystems, the
22 intensification of rainfall on dry bare soils will lead to an increase in runoff and
23 erosion rates, especially on slopes. A common method to reduce erosion is to cover
24 the soil with vegetation. To save costs, this vegetation could be provided by the soil
25 seed bank. Vineyards situated on slopes are part of the typical Mediterranean
26 landscape; thus, developing vegetation cover inside vineyards could be a solution to
27 fight growing erosion risks in addition to providing other valuable services. However,
28 the relationship between slope, erosion and seed loss can vary. Another key
29 ingredient in the development of spontaneous vegetation cover is the spatial
30 dispersal of seeds from one place to another, but the amount of seeds displaced
31 depends on their respective dispersal modes. In this study, we sampled the soil seed
32 bank at two sites characterized by either a low or high frequency of vegetation
33 removal. The soil seed bank was sampled along a transect starting upslope of the
34 vineyards to the bottom of neighboring agricultural ditches. Germination trials were
35 carried out to define the soil seed bank in terms of species and seed density. Each
36 identified species was linked with a main dispersal mode. Our main objective was to
37 assess the effect of vegetation cover on seed loss inside a vineyard, as well as the
38 potential differences in the soil seed bank along our transect and the influence of
39 dispersal mode on those differences. Despite previous contradictory literature,
40 vegetation did not seem to protect interrows from seed loss caused by runoff.
41 Overall, our results support the use of the soil seed bank to provide spontaneous
42 vegetation cover to limit present and future erosion rates and advocate for relaxing

43 vegetation removal operations.

44

45 Keywords: soil seed bank, germination method, dispersal, agrosystem

46 1. Introduction

47 In the Mediterranean area, rainfall events are predicted to become more intense and
48 droughts more severe due to climate change (Cozannet et al., 2022). In
49 agrosystems, rainfall events will increase soil erosion caused by runoff, a
50 phenomenon already considered problematic for more than three decades (Busico et
51 al., 2023). Soil erosion causes multiple problems leading to a decrease in agricultural
52 productivity (Pimentel & Burgess, 2013). A common practice to reduce erosion is to
53 protect the soil with vegetation cover (Wu et al., 2020; Baraibar et al., 2021).

54 The presence of vegetation inside agrosystems would have additional
55 benefits alongside erosion reduction. This idea is at the core of the concept of land
56 sharing, which advocates for maintaining and/or increasing the surface of
57 noncultivated zones found within agrosystems (i.e., hedgerows, field edges, ditches,
58 etc.) (Green et al., 2005; Fischer et al., 2014). To be effective, land sharing requires
59 a sufficient pool of plant biodiversity. This pool can originate from the biodiversity in
60 adjacent habitats or directly from the soil seed bank (Erfanzadeh et al., 2010); thus,
61 seeds can disperse through space or time (Plue and Cousins, 2018).

62 Using the soil seed bank to produce vegetation cover could be considered,
63 but erosion has been associated with seed loss inside the field (Han et al., 2011;
64 Janeau et al., 2022); thus, the potential of spontaneous vegetation cover could be
65 threatened by the process it aims to reduce. Moreover, while the link between
66 erosion and seed loss has been observed to be direct (García-Fayos, Bochet and
67 Cerdà, 2010; Bochet, 2015), seed loss can also occur without erosion when light
68 seeds are removed by runoff water whose force is otherwise too weak to displace
69 soil particles (de Rouw et al., 2018); thus, vegetation cover may reduce erosion but
70 not seed loss. To summarize, runoff can potentially reduce the potential of the soil
71 seed bank to produce sufficient vegetation cover regardless of the surface state.

72 Most studies of the soil seed bank in agrosystems revolve around avoiding
73 seeds from the soil seed bank from germinating to limit weeds in agrosystems (Mahé
74 et al., 2021; Zhang et al., 2021; Adeux et al., 2023). There have been comparisons
75 of the plant diversity between the field and its adjacent zones but those studies
76 mostly investigated the aboveground vegetation (Fried et al., 2012; Minarro, 2012;
77 Barrio et al., 2013; Holland et al., 2017; Cursach et al., 2020), and those that
78 investigated the soil seed bank did not sample outside the cultivated surface
79 (Roschewitz et al., 2005; Fracchiolla et al., 2016; Carpio et al., 2020). Given the lack
80 of linkability between the seed bank and the aboveground vegetation (Andreasen et
81 al 2018), we need to confirm that the difference in diversity between the plot and its
82 surroundings is also found in the seed bank.

83 Together with the field edges, the soil seed bank of agricultural ditches is also
84 not well known. While plant communities inside ditches have been studied

85 (Blomqvist et al., 2006), recent observations of the soil seed bank are lacking.
86 However, ditches are interesting from a restoration perspective because they act as
87 ecological corridors (Herzon and Helenius, 2008; Dollinger et al., 2015); thus, they
88 can accelerate spatial dispersal and improve soil seed bank diversity.

89 Most spatial dispersal modes can be grouped into four main vectors: wind
90 (anemochory), water (hydrochory), animals (zoochory), and gravity (barochory).
91 Usually, spatially dispersed seeds become a part of the soil seed bank (Dekker,
92 1999), but the relative contribution of the different dispersal syndromes to soil seed
93 bank replenishment is still unclear (Benvenuti, 2007). Therefore, studying the soil
94 seed bank could also provide information on the potential plant community and the
95 impact of different dispersal modes on soil seed bank replenishment.

96 To evaluate the potential of vegetation to reduce seed loss and the effect of
97 practices and dispersal modes on the soil seed bank, we set up an experiment to
98 determine the soil seed bank distribution within two Mediterranean vineyards and
99 their adjacent environments, namely, their respective field edges and bordering
100 ditches. The soil seed bank was then described in terms of seed density and species
101 diversity at each sampled point. We formulated three main hypotheses: (1) The
102 effect of the slope on the soil seed bank will be different between tilled and vegetated
103 interrows. We also expect (2) operations within the field to deplete the soil seed
104 bank; thus, the soil seed bank will be denser and more diverse in the field edges and
105 the ditches than within the field. Grouping species into anemochory, hydrochory,
106 barochory, and zoochory, we expect that (3) the effect of slope or position in the
107 study site on the soil seed bank will be different depending on the dispersal mode.

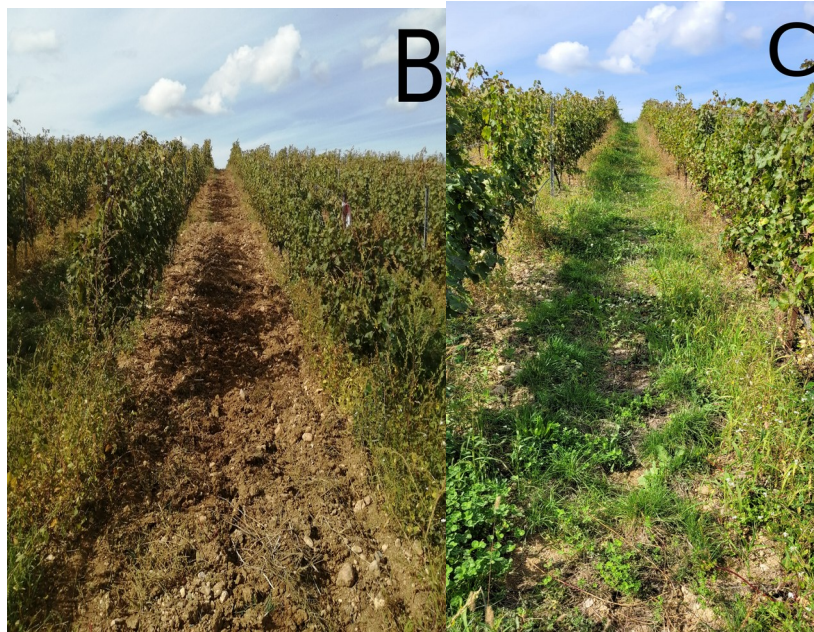
108 2. Materials and methods

109 - 2.1. Study sites

110 Two study sites in the Hérault Department (France) were selected for the experiment
111 (Fig. 1).



114



115
 116 Figure 1. Location of study sites and visualization of interrows in the Roujan study
 117 site (A) and the tilled (B) and vegetated (C) interrows of the Combaillaux study site
 118

119 The first study site, herein designated as the P1, is in the Roujan catchment
 120 (43°30'N, 3°19'E), situated west of Montpellier, France. The Roujan catchment has
 121 been monitored since 1992 as a part of the long-term observatory ORE-OMERE
 122 (Molénat et al., 2018). The Roujan catchment area is a small catchment area (<1
 123 km²) mainly occupied by vineyards framed by a network of drainage ditches dug by
 124 farmers to drain some of the water from the soil, collect runoff and limit erosion. The
 125 catchment is characterized by a sub-Mediterranean subhumid climate with a long dry
 126 period, and the majority of rainfall occurs in spring and autumn. The average rainfall
 127 is 600 mm.year⁻¹ (Molénat et al., 2018). The vineyards that constitute most of the
 128 Roujan catchment area belong to different producers. The maintenance of the
 129 drainage ditches is the responsibility of the owners of the vineyards they cross and
 130 typically consists of removing the vegetation by mowing or burning the vegetation to
 131 preserve the water flow capacity. More rarely, dredging/chemical weeding operations
 132 are carried out. Within the Roujan catchment, P1 is a vineyard of approximately 0.3
 133 ha of *Pinot Noir* grape variety planted on Calcaric Regosols with a mean slope of
 134 approximately 15%. Rows are oriented from east to west. The vineyard is bordered
 135 by other vineyards and a drainage ditch located downstream of the most sloping part
 136 of the vineyard. All interrows of P1 are chemically weeded, and the calendar of
 137 practices has not changed in the last 5 years before the sampling took place. When
 138 sampling took place, P1 was dominated by *Poaceae* and *Brassicaceae* in the field
 139 and the field edge, and by *Rubus fruticosus* inside the ditch.

140
 141 The second study site, referred to as the P2, is in a vineyard situated north of
 142 Montpellier in Combaillaux (UTM 43.659903, 3.767451, first sampled interrow). The
 143 climate there is also classified as Mediterranean and subhumid, with an average
 144 rainfall of approximately 760 mm.year⁻¹. The vineyard is HVE-certified (*Haute Valeur*

145 *Environnementale* - High Environmental Value), which requires a low use of
146 synthetic chemical inputs, a significant share of vegetated interrows, and a share of
147 diversified noncultivated zones situated above a threshold value. P2 has a surface
148 area of approximately 3 ha of *Merlot* grape variety, clay-limestone soil, and a mean
149 slope of approximately 20%. Similar to the P1, rows are oriented from east to west.
150 An agricultural ditch downstream of the vineyard collects run-off water. This ditch
151 separates the vineyard from another field left fallow for part of the year and sowed
152 the remaining time. In this adjacent field, faba beans were sown during soil seed
153 bank sampling. Every second row is mown and plowed after the harvest and then
154 sown, and the remaining rows are simply mown. When sampling occurred, P2 was
155 dominated by a mix of *Fabaceae* and *Poaceae*, and the ditch was mostly composed
156 of *Rubus fruticosus* and *Clematis vitalba*. After sampling in April 2022, a *Trifolium*
157 mixture was sown, and the faba bean seedlings produced by the adjoining land were
158 sown in September 2022.

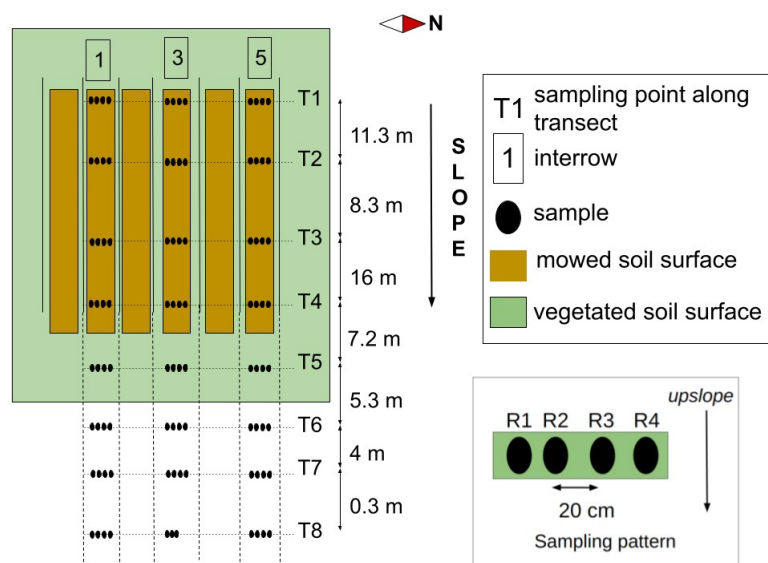
159 As the soil seed bank could be influenced by its surrounding areas, we
160 estimated landscape diversity inside a 500-m radius buffer around the study site
161 following the methodology from Carpio et al. (2020). We classified orthoimages from
162 2021 (source: IGN) in vineyards, other agricultural land and seminatural habitats to
163 obtain the surface proportion of each land cover. We digitized surrounding fields
164 mainly composed of agricultural ditches to obtain a cumulative linear length inside
165 the radius. Consequently, P1 is primarily composed of other vineyards
166 (approximately 70%) and other agricultural lands (approximately 20%), with a small
167 amount of seminatural habitats (approximately 10%). The buffer encompasses more
168 than 8 km of agricultural ditches. P2 is composed of vineyards (approximately 55%)
169 and seminatural habitats (approximately 40%). The buffer encompasses
170 approximately 3 km of agricultural ditches.

171
172 Soil analyses were conducted at both study sites on soil samples taken
173 alongside the soil seed bank samples. Samples were analyzed for pH, total carbon
174 and nitrogen, organic matter content, cation exchange capacity, and concentrations
175 of P, Mg and Na. Data were ultimately removed from the analysis due to a lack of
176 significant results (Appendix A).

177 178 - 2.2. Soil seed bank sampling protocol

179
180 Soil seed bank sampling was carried out along a 50-meter transect consisting
181 of 8 points starting upslope within the field until the ditch at the bottom of the study
182 site. The first four sampling points are situated within the field, with T1 at the top of
183 the slope and T4 at the bottom of the slope. Sampling was carried out using a corer
184 that allowed the sampling of 10 cm diameter cylinders at a depth of 10 cm. The
185 number of interrows sampled was determined so we had at least 3 interrows with the
186 same vegetation state. For each point, 4 samples were collected. In the P1, 3
187 interrows were sampled with a spacing of one interrow between each of them (Fig.
188 2). The first row of the vineyard was not sampled to avoid edge effects. In total, the

189 sampling area covered approximately 350 m²



190

191 Figure 2. Representation of the Roujan vineyard (P1) and sample distribution. Each sample point represents 4
 192 samples taken on a straight line approximately 20 cm from each other.

193

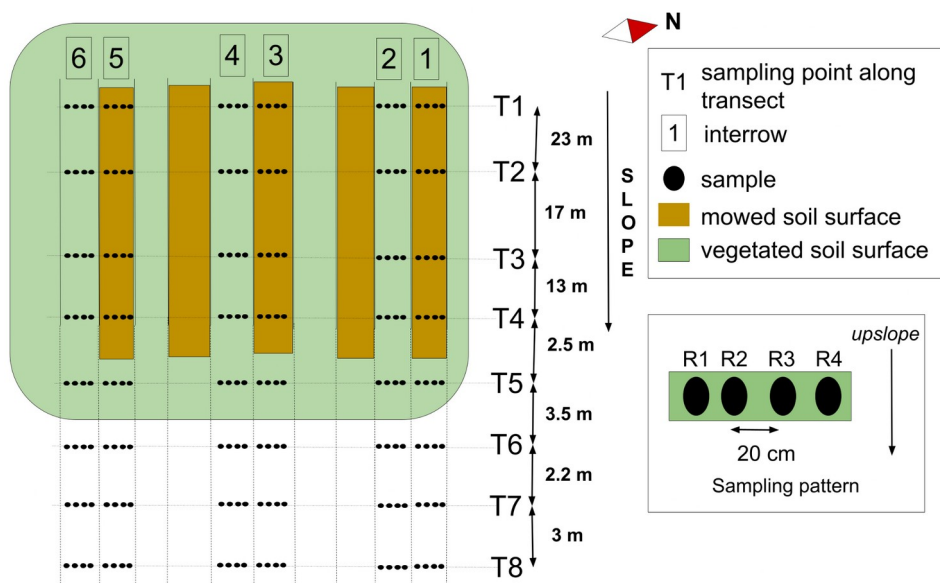
194 In the P2, 6 interrows were sampled, one with permanent plant cover and the other
 195 plowed after harvest (around mid-September) and then sown in April 2022. The
 196 sampling area covered approximately 2000 m² (Fig. 3).

197

198 In total, 286 soil samples were collected for the soil seed bank of the two study sites,
 199 representing 9 interrows, 8 sampling points and 4 replicates at each sampling point,
 200 except one in the P1, where we were only able to collect 2 soil samples because the
 201 soil layer was too thin to collect the other two samples.

202

203



204

205 Figure 3. Representation of the Combaillaux vineyard (P2) sampling distribution and detailed sampling pattern.
 206 Each sample point represents 4 samples taken on a straight line approximately 20 cm from each other.

207

208 - 2.3. *Seedling emergence method*

209

210 Three days after the collection of the soil samples in the field (in April 2022), the 286
211 soil samples were placed in perforated plastic boxes (200x170x75 mm) on a layer of
212 draining sand and covered with potting soil to facilitate germination. Before use, the
213 potting soil was sterilized to ensure that it did not contain any organisms that could
214 influence the development of the seeds (granivores, fungi, insects, etc.). The
215 sterilization process included successive oven drying and then freezing the soil. The
216 boxes were then placed randomly in an air-conditioned greenhouse (average $T^{\circ} = 22$
217 $\pm 3^{\circ}\text{C}$) on 3 separate benches. To ensure that the samples were not contaminated
218 by exogenic seed input or seeds from other samples, one control box containing only
219 sand and potting soil was placed on each bench. The samples were manually
220 irrigated 5 days a week with tap water to maintain a constant moisture content
221 throughout the experiment.

222 To trigger the emergence of the seeds of certain species from dormancy, a
223 cold stratification period at 1°C was carried out for one month. The boxes were then
224 placed back in the greenhouse in a randomized arrangement different from that prior
225 to vernalization. The samples were also shuffled to stimulate germination (Price et
226 al., 2010; Erfanzadeh et al., 2016).

227 Samples were monitored regularly to count and remove individuals sufficiently
228 developed to be identifiable at the species level if possible and at the genus level
229 otherwise using the Latin nomenclature as available in the WFO Plant List
230 classification (<https://wfoplantlist.org/plant-list/>). Poaceae were regularly replanted in
231 individual pots to achieve a more precise identification without impacting the
232 remaining seeds that may still germinate within the samples.

233 The spontaneous germination experiment took place over nine months. It was
234 divided into two cycles: from April 2022 to July 2022 and from September 2022 to
235 December 2022. The end of the experiment occurred after 2 weeks with the absence
236 of seed emergence. Residual soil was not combed because the added information
237 has been considered negligible in previous studies (Niknam et al., 2018).

238

239 - 2.4. *Soil seed bank sampling representativity*

240

241 To gain insight into how many species we might have missed, we used calculations
242 developed for plant species composition surveys. This method is based on
243 computing the theoretical species accumulation curve (SAC) by calculating the sum
244 of generalized Simpson entropies based on subsampling using jackknife methods
245 (Zhang and Zhou, 2010, summarized in Marcon, 2015). This method forecasts the
246 effort needed to reach the “true” number of species in the sampled population.
247 According to this method, we could have missed approximately 10 species in our
248 sampled soil seed bank, which means that our results might have a bias of
249 approximately 10%.

250

251 - 2.5. *Dispersal modes*

252

253 Species observed throughout the emergence period have been linked to their main
254 dispersal mode using the TRY database (Kattge et al., 2020). Most species had
255 several dispersal modes; thus, the most observed mode was selected. Among the
256 96 different species identified, 16 were primarily dispersed by anemochory, 11 by
257 barochory, 15 by hydrochory and 54 by zoochory.

258

259 - 2.6. Statistical analyses

260

261 Eight different equations were used for generalized linear model (GLM)
262 construction (Tab. 1), with separate GLMs constructed for each study site.

263 All data manipulation and statistical analyses were performed using R 4.2.2 (R Core

264 Team, 2023) software. The Shannon index was computed for every sample using

265 the entropart package (Marcon and Hérault, 2015) with a Chao, Wang & Jost

266 correction (Chao, Wang and Jost, 2013) to take undetected species into account.

267 The number of germinated seeds observed per box (=E) was related to the area

268 sampled (=S, equal to 0.008 m²). Thus, the number of germinated seeds per surface

269 unit obtained for each box, referred to as the "E/S ratio" (in number of plants per

270 m²), was used for statistical analysis (Gaudichet et al., 2022). Vegetation cover was

271 visually inspected at multiple points in every interrow sampled. In the Combaillaux

272 vineyard, vegetation cover was on average between 90 and 100% inside the

273 vegetated interrows and under 5% inside the unvegetated interrows. In the Roujan

274 vineyard, vegetation cover was on average under 5% in all the studied interrows.

275 Consequently, the analyses that included the effect of vegetation cover were only

276 conducted on data collected within the field in the P2, and vegetation cover was

277 included as presence/absence data in the models. Concerning the effect of dispersal

278 mode on soil seed bank distribution, the number of germinated seeds observed for

279 each main dispersal mode dispersal mode defined in the previous section was

280 weighted by the number of species with this dispersal mode to avoid having an

281 inflated E/S ratio caused by an overrepresentation of one particular dispersal mode.

282 The effect of the slope on the soil seed bank was tested using samples taken

283 from the first 4 sampling points, which were used as a proxy for the slope gradient

284 within the field. The sampled transect points were grouped into three zones: points

285 T1 to T4 in the field (*field* zone), points T5 to T7 in the field edge (*field edge* zone),

286 and points taken in T8 (*ditch* zone).

287 The effect of landscape was not analyzed since the information would have

288 been identical for every sample in each study site.

289

290 Because the number of germinated seeds was not normally distributed, our

291 hypotheses were tested by constructing GLMs with a Poisson distribution, which

292 eliminates the requirement for linearity and homoscedasticity of the data.

293 Overdispersion of the residuals was detected; thus, a correction was applied using a

294 quasi-GLM (Zuur et al., 2009). Based on a visual inspection, normality of the

295 residuals and homogeneity of variances were met. Models were then tested using

296 ANOVA tests.

297 To confirm that greenhouse position did not impact emergence, a GLM linking
298 the E/S ratio to the sample location within the greenhouse was also constructed and
299 tested with ANOVA. Greenhouse position did not have an impact on the number of
300 seeds that germinated ($F = 0.44$, $p = 0.66$).

301

302 Table 1. Variables used for generalized linear model (GLM) construction. Separate GLMs were constructed for
303 the two study sites, except for Equations 5 and 6, including the effect of the vegetation cover, which were only
304 constructed using data from inside the field of the Combaillaux study site. Vegetation cover was included as
305 presence/absence data in the models

Eq	Y	Explanatory variable(s)
1	E/S ratio	slope
2	Shannon index	slope
3	E/S ratio	zone
4	Shannon index	zone
5	E/S ratio	Interaction between zone and vegetation cover
6	Shannon index	Interaction between zone and vegetation cover
7	E/S ratio	Interaction between zone and dispersal mode
8	Number of species over the total number of species for the dispersal mode	zone

306

307

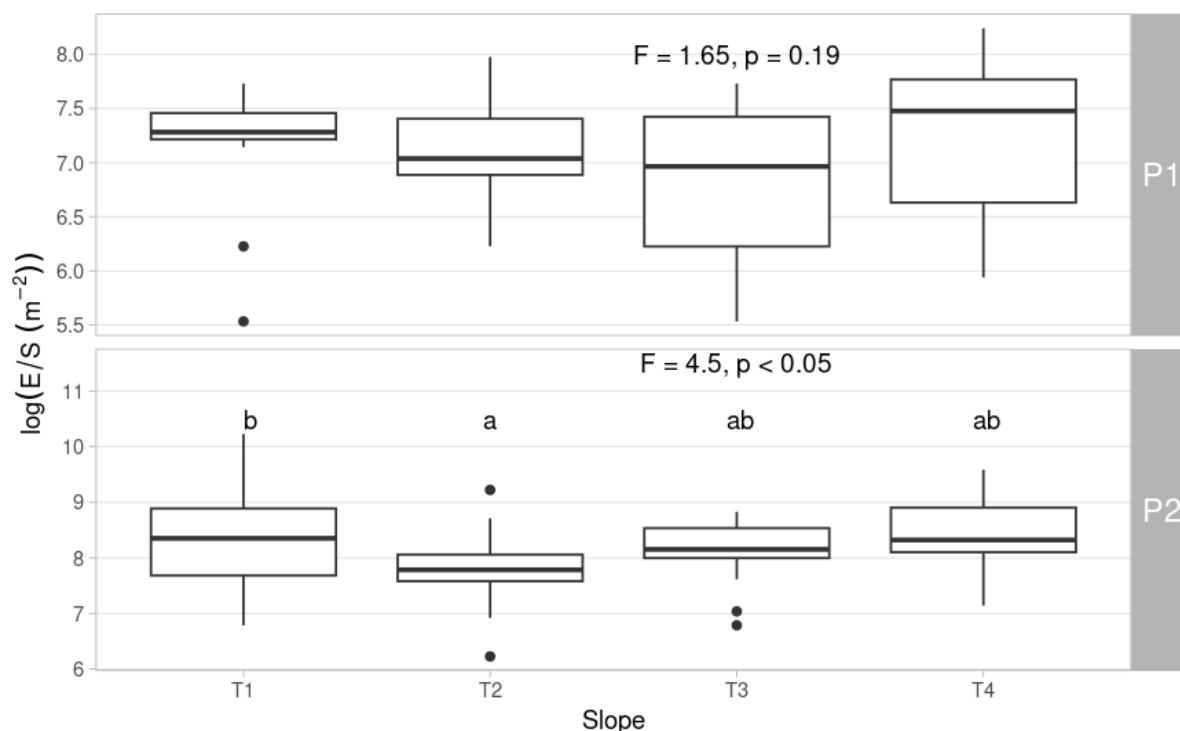
308 Differences between the coefficients computed for each GLM were tested by
309 performing post hoc Tukey tests with the emmeans package (Lenth et al., 2023).

310 3. Results

311 A total of 96 species were identified during our experiment, 52 of which were found
312 in both study sites (Tab. 2).

313

314 In the P2, the E/S ratio in T1 (upslope) was significantly higher (6160 ± 6203
315 seedlings/m²) than the E/S ratio in T2 (steepest part of the slope) (2900 ± 1969
316 seedlings/m²). However, we could not show such an effect of slope in P1 (Fig. 4).



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Figure 4. Distribution of the E/S ratio (in log scale) by sampling point within the field for P1 (Roujan vineyard) and P2 (Combaillaux vineyard). The slope effect was tested by ANOVAs on two separate GLMs constructed with data collected in P1 and the P2. T1 is situated before the start of the slope, T2 is at the start of the slope, T3 is at the end of the slope and T4 is at the bottom of the slope. In the plot displaying data from the P2, different letters indicate a significant difference between GLM coefficients.

Table 2. Number of species, first five most observed species and their respective contribution in samples found in each study site, in both study sites, and overall

	P1 <i>Roujan vineyard</i>	P2 <i>Combaillaux vineyard</i>	Shared	Total
Number of species observed	68	81	52	96
Most observed species	<i>Diplotaxis erucoides</i> (10.6%)	<i>Setaria pumila</i> (13.3%)	<i>Setaria pumila</i> (12.1%)	<i>Setaria pumila</i> (11.1%)
2nd most observed species	<i>Euphorbia prostrata</i> (9.3%)	<i>Portulaca oleracea</i> (12%)	<i>Euphorbia prostrata</i> (11.6%)	<i>Euphorbia prostrata</i> (10.7%)
3rd most observed species	<i>Poa annua</i> (9%)	<i>Chenopodium album</i> (11.5%)	<i>Portulaca oleracea</i> (10.3%)	<i>Portulaca oleracea</i> (9.5%)
4th most observed species	<i>Erigeron sumatrensis</i> (7%)	<i>Euphorbia prostrata</i> (11.2%)	<i>Chenopodium album</i> (10.1%)	<i>Chenopodium album</i> (9.3%)

5th most observed species	<i>Lysimachia foemina</i> (6%)	<i>Polygonum aviculare</i> (8.5%)	<i>Polygonum aviculare</i> (7.2%)	<i>Polygonum aviculare</i> (6.6%)
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3.1. In-field effect of vegetation cover

328

329 The mean E/S ratio was significantly higher in samples originating from vegetated
330 interrows (5329 +/- 4419 seedlings/m²) than in samples originating from tilled
331 interrows (3773 +/- 3109 seedlings/m²; t = 1.99, p<0.05).

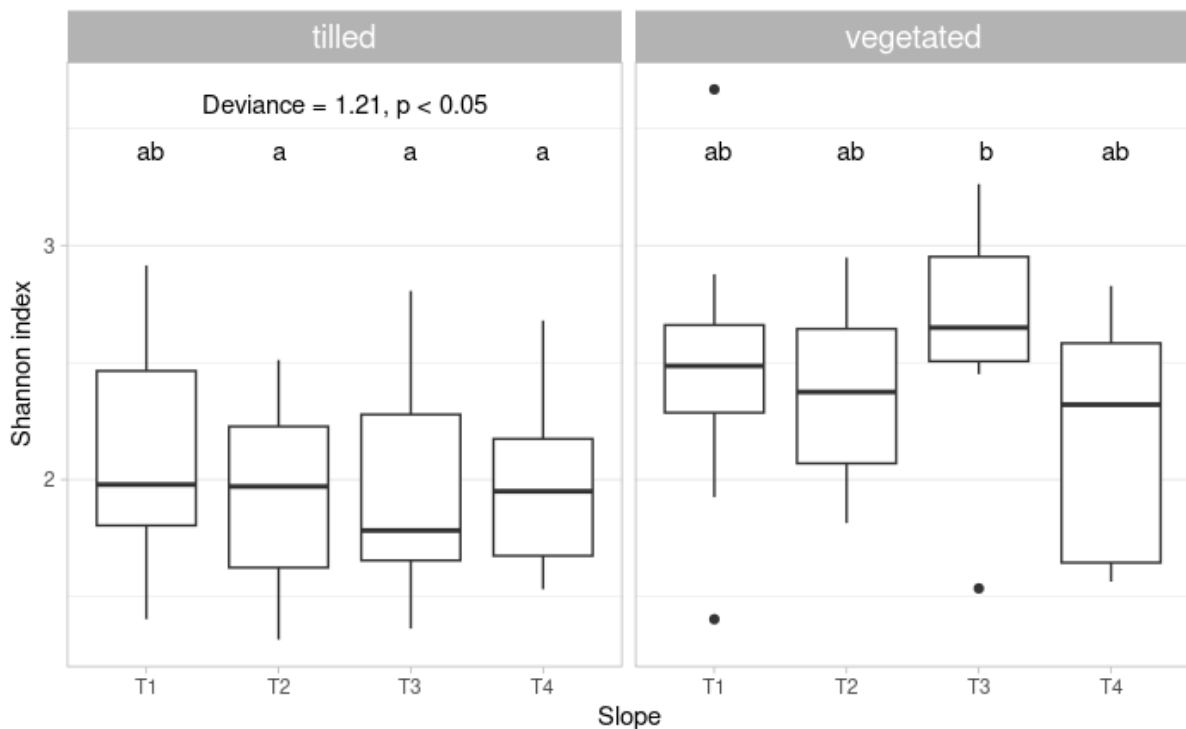
332 The mean Shannon index was also significantly higher in samples originating from
333 vegetated interrows (2.42 +/- 0.48) than in samples originating from tilled interrows
334 (1.99 +/- 0.41; t = -4.61, p<0.01).

335

336 We could not show a significant interaction of slope and vegetation cover on the E/S
337 ratio (F = 1.9, p = 0.12).

338 However, the interaction of slope and vegetation cover had a significant positive
339 effect on the Shannon index (Fig. 5). The mean Shannon index from T3 (slope end)
340 was significantly lower (1.95 +/- 0.43) in tilled interrows than in vegetated interrows
341 (2.67 +/- 0.46; p < 0.01).

342



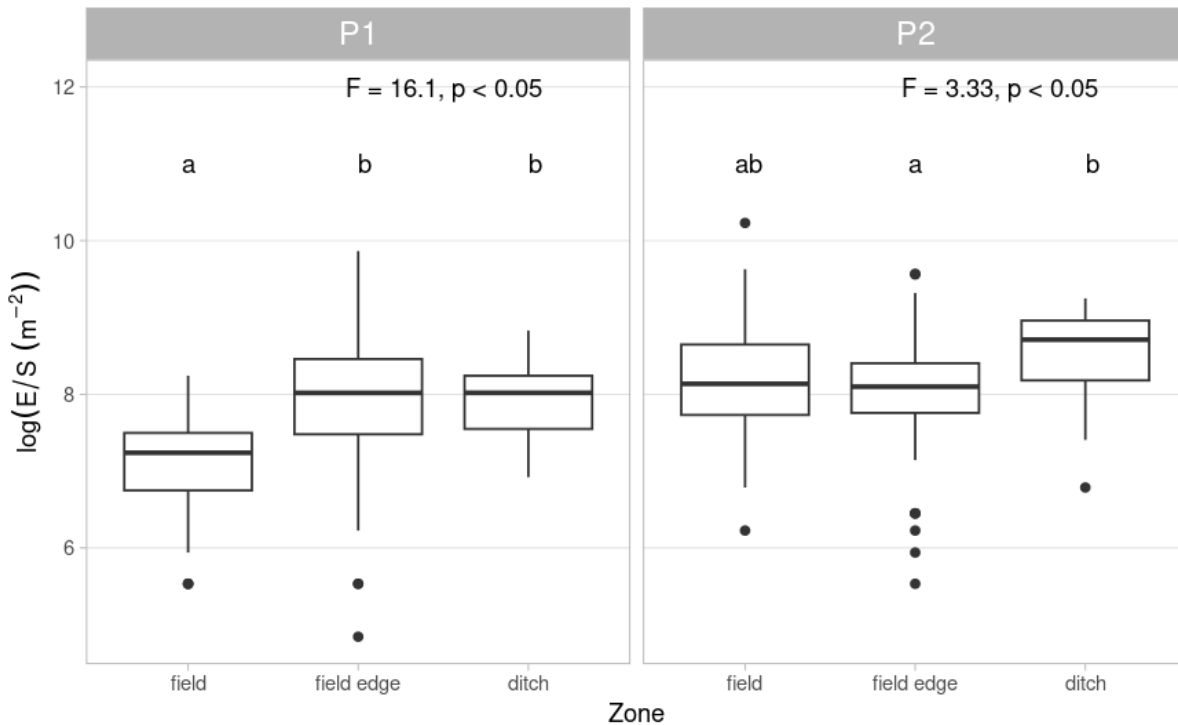
343

344 Figure 5. Shannon index computed for each sample grouped by slope point sampled for P2 (Combaillaux
345 vineyard) only in tilled and vegetated interrows. The combination of the slope point and the presence of
346 vegetation on the Shannon index was tested with ANOVA. T1 is situated before the start of the slope, T2 is at the
347 start of the slope, T3 is at the end of the slope and T4 is at the bottom of the slope. The difference between all
348 coefficients was tested with Tukey tests between all slope points, and different letters are used when differences
349 are significant.

350 3.2. Zone effect

351 - 3.2.1. Effect of zone on the E/S ratio

352 Zone (i.e., the sample origin between the field, field edge and ditch) had a significant
353 effect on the E/S ratio at both study sites. In the P1, the mean E/S ratio was lower
354 within (1426 +/- 803 seedlings/m²) than outside the field (field edge: 3860 +/- 3953
355 seedlings/m²; ditch: 3144 +/- 1524 seedlings/m²). In the P2, the mean E/S ratio was
356 lower at the field edge (3839 +/- 2760 seedlings/m²) than in the ditch (5759 +/- 2755
357 seedlings/m²; Fig. 6).



358

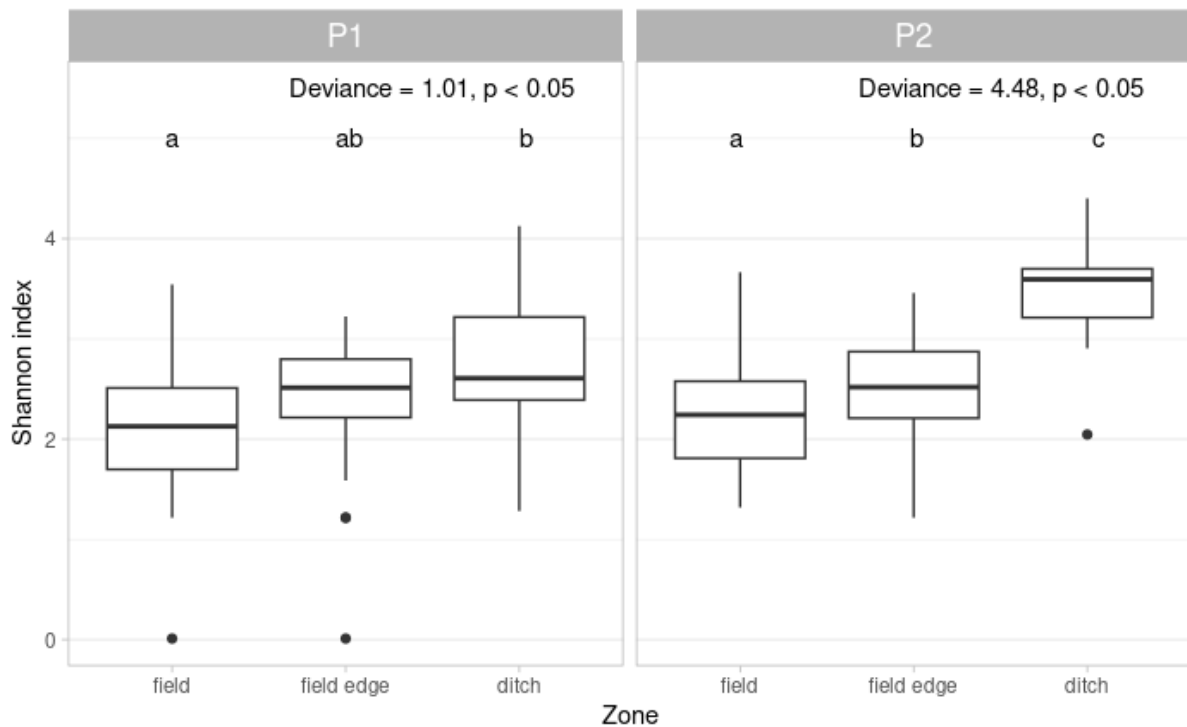
359 Figure 6. Distribution of the E/S ratio (in log scale for readability purposes) in each sample, grouped by location in
360 the study site, for P1 (Roujan vineyard) and P2 (Combaillaux vineyard) separately. The “field” location represents
361 samples taken within vineyard rows, the “field edge” location represents samples taken between the rows and
362 the ditch, and the “ditch” location represents samples taken within agricultural ditches. The location effect was
363 tested with ANOVAs, the difference between coefficients was tested with Tukey tests, and different letters are
364 used when differences are significant.

365

366 - 3.2.2. Effect of zone on the Shannon index

367

368 Zone had a significant effect on the Shannon diversity index at both sites (Fig. 7).
369 In the P1, the mean Shannon index was only significantly higher in the ditch (2.74 +/-
370 0.65) than in the field (2.13 +/- 0.64, $p < 0.05$), whereas in the P2, both the field edge
371 (2.48 +/- 0.49, $p < 0.01$) and the ditch (3.49 +/- 0.49, $p < 0.01$) had a higher mean
372 Shannon index than the field (2.20 +/- 0.49). The mean Shannon index was also
373 significantly higher in the ditch than in the field edge (Fig. 7).



374

375 Figure 7. Shannon index computed for each sample grouped by location sampled for P1 (Roujan vineyard) and
 376 P2 (Combaillaux vineyard). The “field” location represents samples taken within vineyard rows, the “field edge”
 377 location represents samples taken between the rows and the agricultural ditch, and the “ditch” location
 378 represents samples taken within the agricultural ditches. The location effect was tested with ANOVAs.
 379 Differences between coefficients were tested with Tukey tests, and different letters are used when differences
 380 are significant.

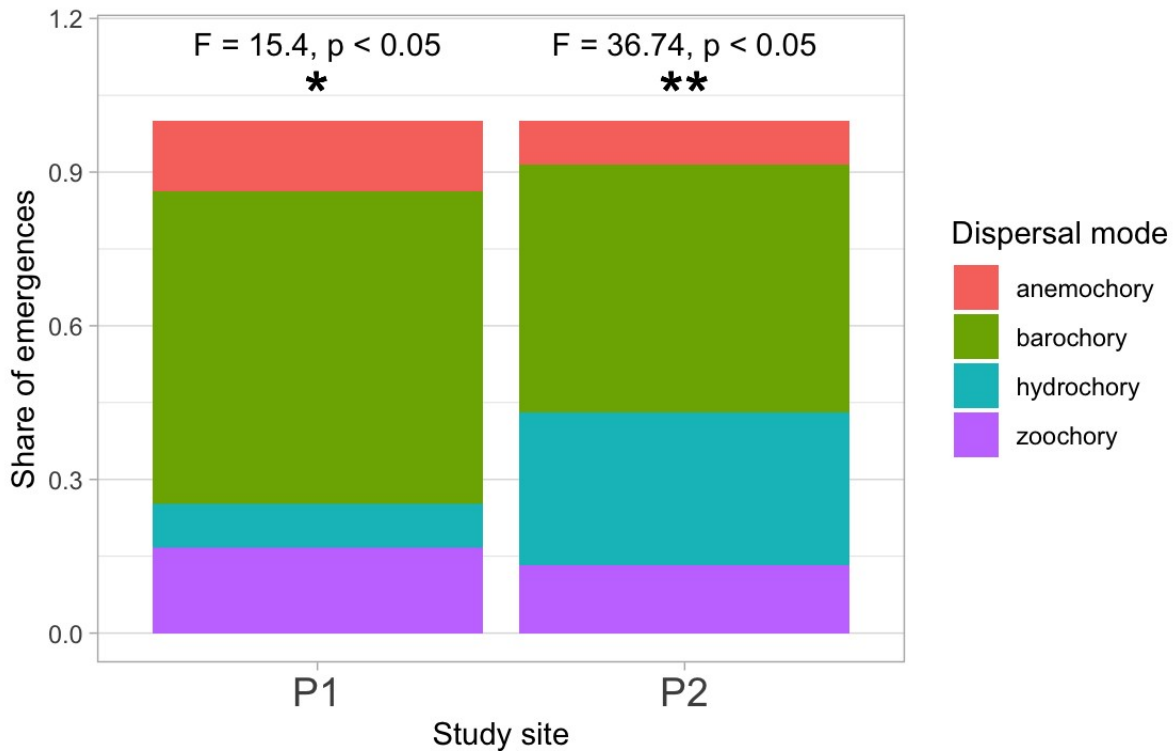
381 3.3. Effect of dispersal mode on the soil seed bank

382 - 3.4.1. Effect of dispersal modes on the E/S ratio

383 The dispersal mode affected the overall E/S ratio observed at both study sites (Fig.
 384 8). At both sites, barochory was more prevalent than other dispersal modes (Fig. 8).
 385 Additionally, in the P2, hydrochory was more prevalent than anemochory and
 386 zoochory (Fig. 8; Appendix B).

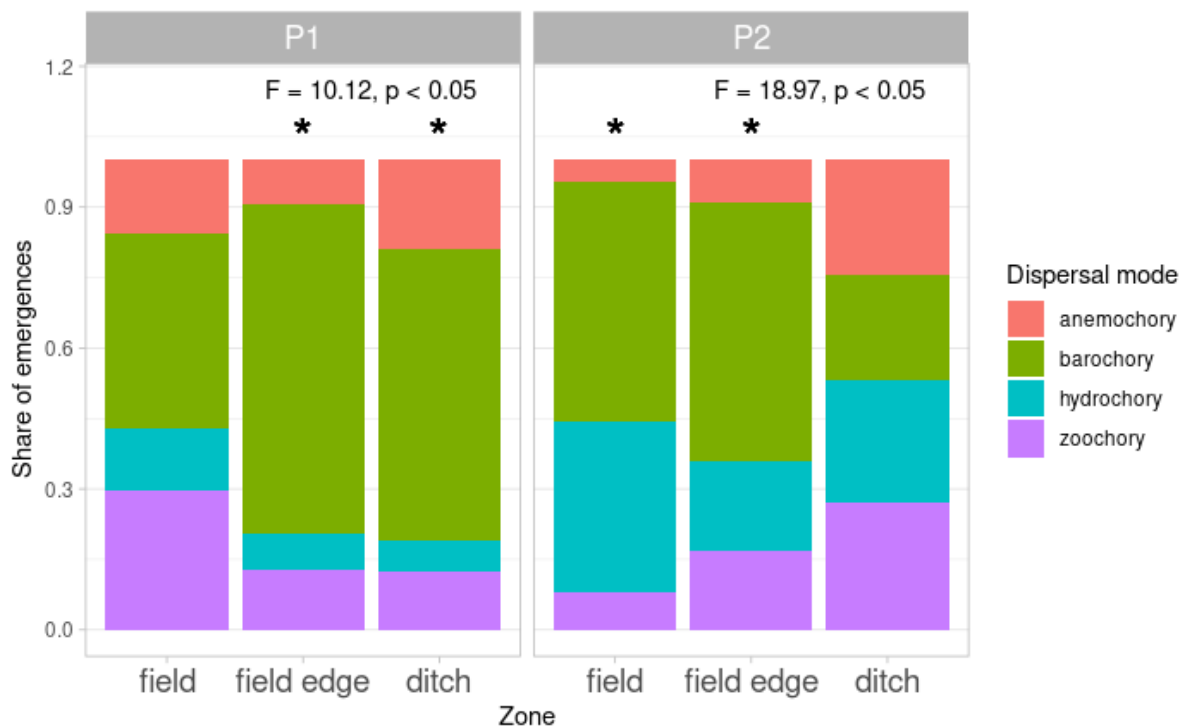
387 The dispersal mode had a significant effect on the E/S ratio observed in each
 388 zone for both study sites (Fig. 9; Appendix B).

389 In the P1, barochory was more prevalent than other dispersal modes at the
 390 field edge and in the ditch. In the P2, anemochory and zoochory were rarer than
 391 barochory and hydrochory in the field. Zoochory was also rarer than barochory at the
 392 field edge, and barochory was more frequent than hydrochory (Fig. 9; Appendix B).



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Figure 8. Share of emergences for each dispersal mode for P1 (Roujan vineyard) and P2 (Combaillaux vineyard) separately. Significant differences between dispersal modes using Tukey tests are represented using stars, one for each dispersal mode significantly different from the others.



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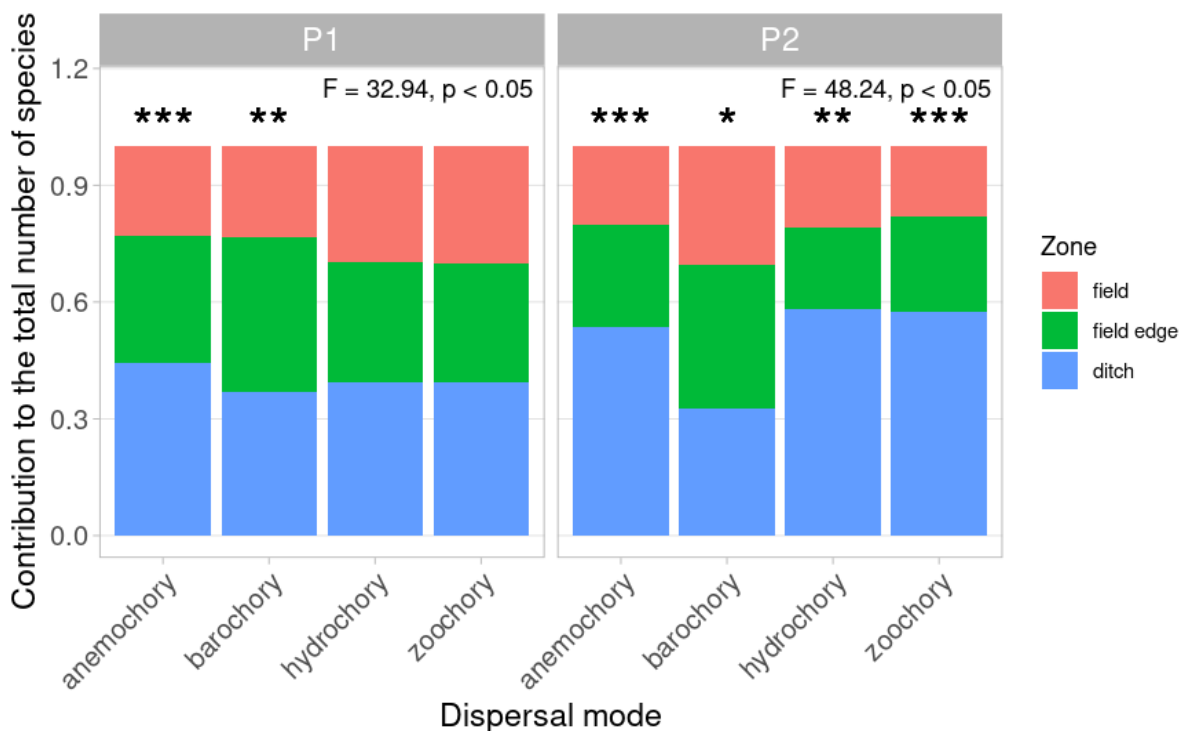
Figure 9. Mean E/S ratio by species for each dispersal mode, grouped by zone sampled, for P1 (Roujan vineyard) and P2 (Combaillaux vineyard). The “field” location represents samples taken within vineyard rows, the “field edge” location represents samples taken between the rows and the agricultural ditch, and the “ditch” location represents samples taken within the agricultural ditches. Significant differences between dispersal modes using Tukey tests are represented using stars, one for each dispersal mode significantly different from the others.

405 - 3.4.2. Influence of dispersal modes on the number of species

406 The dispersal mode had a significant effect on the number of species found in each
 407 zone at both study sites. More anemochorous species were observed outside the
 408 field than within both study sites. Additionally, the maximum number of
 409 anemochorous species was found within the ditch in both study sites. Last, more
 410 barochorous species were found in the field edge than in the field for both study sites
 411 (Fig. 10; Appendix B).

412

413 In the P1, more barochorous species were found in the ditch than in the field.
 414 In the P2, the ditch hosted more hydrochorous species than the field and the field
 415 edge. Similarly, fewer zoochorous species were observed in the field than in the field
 416 edge and the ditch, and there were also fewer zoochorous species in the field edge
 417 than in the ditch (Fig. 10; Appendix B).



418

419 Figure 10. Contribution of each zone to the total number of species, grouped by dispersal syndrome, for P1
 420 (Roujan vineyard) and P2 (Combaillaux vineyard) separately. Significant differences between zones using Tukey
 421 tests are represented using stars, one for each zone significantly different from another.

422 **4. Discussion**

423 **4.1. Effect of vegetation cover in interrows on seed loss**
 424 **reduction**

425

426 Our first hypothesis that the effect of the slope on soil seed bank density would be
 427 different between tilled and vegetated interrows was not supported. This result
 428 coincides with other works observing an absence of a link between seed loss and

429 erosion (de Rouw et al., 2018). In their study, de Rouw et al. (2018) explained the
430 possibility for seeds to be dispersed without the occurrence of soil erosion by the
431 lower discharge necessary to move small and light seeds compared to the threshold
432 value over which erosion starts, which might be the explanation for our results.

433 Nevertheless, the overall higher number of seeds that germinated in
434 vegetated interrows and the higher species diversity gives credit to the expected
435 benefits of vegetation cover on sloping conditions, which are more diverse than
436 erosion control. While the benefits of vegetation cover on the soil seed bank of
437 woody crops have already been observed in different orchards (Carpio et al., 2020),
438 the spatial configuration of a vineyard and the slope are differences important
439 enough to consider these results noteworthy.

440 4.2. Soil seed bank diversity along the transect

441
442 The soil seed bank was found to be denser within the ditch than in the field in Roujan
443 but not in Combaillaux. Our second hypothesis that the soil seed bank would be
444 denser and more diverse inside the field margins and ditches than within the field
445 was thus partially validated. Since chemical weeding inside the field is prevalent in
446 Roujan and nonexistent in Combaillaux, it could be the factor that explains this
447 difference between sites. Indeed, chemical weeding has been linked with soil seed
448 bank depletion in previous studies (Andreasen et al., 2018).

449 The higher species diversity in the ditch found in both study sites is in
450 accordance with the literature obtained on aboveground vegetation studies (Fried et
451 al., 2012; Minarro, 2012; Holland et al., 2017; Cursach et al., 2020), which is
452 interesting because the soil seed bank and the aboveground vegetation are not
453 always similar in agrosystems (Andreasen et al., 2018). The results in the
454 Combaillaux vineyard also indicate that interrows benefit from the field edge and the
455 ditch as potential biodiversity sources, while the Roujan vineyard benefits only from
456 the ditch. Thus, reducing chemical inputs benefits both the field and the field edges,
457 which is in accordance with the expectations of land sharing (Fischer et al., 2014).

458 Like landscape in general, other factors, such as altitudinal gradient
459 (Erfanzadeh et al., 2013), need to be accounted for when considering recolonization
460 processes that stem from the soil seed bank of neighboring habitats.

461 Our results also need to be nuanced due to differences between our two
462 study sites in both local conditions: annual precipitation and soil conditions, and the
463 surrounding environment in terms of land uses and cumulative length of ditches. The
464 higher length of ditches in Roujan than in Combaillaux could explain the higher
465 diversity in the ditches, whereas the higher amount of seminatural habitats in
466 Combaillaux could counterbalance the difference between sites. These doubts could
467 be dispelled by implementing a new protocol based on more sites covering the
468 region's soil and climate diversity to study the interparcel variability of the seed bank.
469

470 4.3. Dispersal mode and soil seed bank distribution

471

472 At both sites, dispersal mode played a role in soil seed bank distribution. Our
473 results show that barochory is well represented within vineyards and their
474 surrounding habitats, as was already reviewed by Benvenuti (2007) for agricultural
475 environments in general. Barochory was prevalent outside the field both in terms of
476 seed density and species in Roujan. However, the results were mixed in
477 Combaillaux, where barochory was mostly observed within the field in terms of seed
478 density but outside the field in terms of the number of species. Because the mean
479 slope is 15% in Roujan and 20% in Combaillaux, the beneficial effect of slope on
480 dispersal by barochory is not straightforward in our results. In Combaillaux, it is
481 possible that practices favored a few opportunistic species within the field, whereas
482 conditions outside the field allowed more species with different dispersal modes to
483 develop.

484 Concerning the distribution of hydrochorous species, we only observed more
485 species in the ditch for the Combaillaux site and found no differences in terms of the
486 number of seed counts. The absence of a higher number of hydrochorous species
487 within the ditch in Roujan is likely due to the site position on the upper side of the
488 Roujan catchment, which makes it a likelier site for seed detachment than retention
489 due to its hydrological regime and its slope (Calçada et al., 2015; Fraaje et al., 2017;
490 West et al., 2020; Su et al., 2022). An additional explanation could be the length of
491 the ditch network, which is almost 3 times longer in Roujan than in Combaillaux;
492 thus, seeds have more space to disperse.

493 As agricultural ditches can act as biodiversity corridors and refuges (Herzon
494 and Helenius, 2008; Dollinger et al., 2015), it is not surprising to observe more
495 zoochorous species within the ditch than within the field, although this result was
496 observed only in Combaillaux. In Combaillaux, presence of carabids, small mammals
497 and ants was observed, whereas in Roujan only ants were observed. This difference
498 could be explained by the landscape, especially by the share of seminatural habitats,
499 which is higher in Combaillaux (55%) than in Roujan (10%), because seminatural
500 habitats are important biodiversity refuges (Garibaldi et al., 2021; Tscharntke et al.,
501 2021).

502

503 Conclusion

504

505 To our knowledge, this study was one of the first to study the effect of
506 management practices on the soil seed bank from inside a field to the bottom of an
507 agricultural ditch. Another noteworthy result of this study is the observation that
508 vegetation inside the interrows did not significantly reduce the depleting effect of the
509 slope on the soil seed bank distribution, despite the well-known role of erosion
510 reduction on vegetation and seed loss. These preliminary results, should they be
511 confirmed by further studies, could influence weeding practices in vineyards in order

512 to maximize potential benefits from a rich soil seed bank inside agroecosystems.. To
513 confirm the related hypothesis we made to explain some of our results, further work
514 investigating the influence of landscape on the soil seed bank is needed.

515

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518

519 Acknowledgments

520

521 The authors wish to thank the two anonymous reviewers for their helpful comments,
522 which helped to highlight the strengths of our study. The authors warmly thank Pauline
523 MARTIN and Léo BOULAIS for their high involvement in the seedling emergence
524 experiment. The authors are also very grateful to Léa GENTY, David FAGES, Manon
525 LAGACHERIE, Sandrine NEGRO, and Sébastien TROIANO for their technical support in the
526 experiment and collection of the data. The authors also wish to thank the Environmental
527 Research Observatory OMERE (<http://www.obs-omere.org>), whose policy drives the
528 availability of part of the data used in the current study. Last, the authors wish to thank the
529 vinegrowers for giving them access to their vineyards.

530

531 The PhD of M.F. was funded through LabEX AGRO 2011-LABX-002 (under the I-Site
532 Muse framework) coordinated by Agropolis Fondation. The experimental part of the study
533 was funded by both LabEX AGRO 2011-LABX-002 and INRAE Metaprogram Biosefair (AMI-
534 2021). For the purpose of Open Access, a CC-BY public copyright license has been applied
535 by the authors to the present document and will be applied to all subsequent versions up to
536 the Author Accepted Manuscript arising from this submission.

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Field	Interrow	Transect	PH	CARBONE (g/kg)	SOM (g/kg)	N (g/kg)	C/N	PHOSPHATE	MAGNESIUM	MgO (mg/kg)	POTASSIUM
P1	1	T1	8.3	11.6	19.95	1.3	8.92	155	7.7	155.16	3.72
P1	1	T2	8.5	9	15.48	0.69	13.04	93	6.53	131.58	2.77
P1	1	T3	8.2	17.4	29.93	1.31	13.28	163	11.64	234.55	9.73
P1	1	T4	8.6	11.3	19.44	0.92	12.28	131	9.15	184.37	5.79
P1	1	T5	8.3	15.3	26.32	1.29	11.86	114	10.84	218.43	6.29
P1	1	T6	8.3	17.7	30.44	1.54	11.49	136	11	221.65	6.21
P1	3	T1	8.5	10.2	17.54	0.82	12.44	89	09.09	183.16	3.16
P1	3	T2	8.5	10.2	17.54	0.8	12.75	85	7.58	152.74	4.23
P1	3	T3	8.6	9.3	16	0.9	10.33	84	7.25	146.09	3
P1	3	T4	8.5	15.5	26.66	1.4	11.07	276	10.09	203.31	7.15
P1	3	T5	8.5	16	27.52	1.38	11.59	104	12.19	245.63	5.9
P1	3	T6	8.3	17.3	29.76	1.64	10.55	111	10.91	219.84	5.3
P1	5	T1	8.1	25.3	43.52	2.26	11.19	221	10.7	215.61	5.88
P1	5	T2	8.5	12.1	20.81	01.01	11.98	95	10.23	206.13	3.33
P1	5	T3	8.5	11	18.92	0.81	13.58	91	7.31	147.3	03.03
P1	5	T4	8.3	9.6	16.51	0.91	10.55	92	6.74	135.81	04.01
P1	5	T5	8.1	17.8	30.62	1.37	12.99	100	9.15	184.37	11.35
P1	5	T6	8.5	8.8	15.14	01.03	8.54	98	7.19	144.88	4.15
P2	1	T1	8.3	22.9	39.39	1.89	12.12	127	11.19	225.48	4.51
P2	1	T2	8.6	17.3	29.76	1.2	14.42	192	10.43	210.16	5.54
P2	1	T3	8.6	11.7	20.12	0.73	16.03	59	14.7	296.21	4.21
P2	1	T4	8.5	12.1	20.81	1	12.1	123	9.77	196.87	05.06
P2	1	T5	8.3	19.3	33.2	1.5	12.87	247	12.64	254.7	9.58
P2	1	T6	8.1	27.5	47.3	2.35	11.7	311	13.8	278.07	12.59
P2	1	T7	8.3	22.7	39.04	1.58	14.37	208	11.2	225.68	7.61
P2	3	T1	8.2	29.2	50.22	1.97	14.82	196	11.4	229.71	8.58
P2	3	T2	8.5	17.6	30.27	1.38	12.75	206	12.16	245.02	7.67
P2	3	T3	8.4	19.3	33.2	1.45	13.31	188	13.15	264.97	10.02
P2	3	T4	8.2	19.1	32.85	1.42	13.45	280	12.1	243.82	7.87
P2	3	T5	8	24.1	41.45	1.98	12.17	264	13.67	275.45	11.18
P2	3	T6	8.3	26.9	46.27	1.61	16.71	235	14.38	289.76	12.58
P2	5	T1	8.5	14.9	25.63	0.99	15.05	147	10.48	211.17	6.77
P2	5	T2	8.5	14.1	24.25	0.92	15.33	77	11.2	225.68	6.96
P2	5	T3	8.5	9.8	16.86	0.73	13.42	62	10.05	202.51	5.37
P2	5	T4	8.4	15	25.8	0.98	15.31	163	11.05	222.66	7.6
P2	5	T5	8.2	20.4	35.09	1.59	12.83	253	11.93	240.39	10.76
P2	5	T6	8.4	15.2	26.14	1.14	13.33	94	8.46	170.47	4.96
P2	5	T7	8.2	26.8	46.1	2.23	12.02	180	11.49	231.52	7.41
P2	2	T1	8.6	9.9	17.03	0.76	13.03	63	8.54	172.08	3.27
P2	2	T2	8.5	10.3	17.72	0.86	11.98	60	10.74	216.41	4.85
P2	2	T3	8.5	13.6	23.39	1.1	12.36	110	9.83	198.07	6.73
P2	2	T4	8.3	18.9	32.51	1.4	13.5	233	9.67	194.85	9.68
P2	2	T5	8	24.6	42.31	1.91	12.88	187	10.87	219.03	08.04

P2	2	T6	8.4	14.3	24.6	01.02	14.02	124	8.59	173.09	5.66
P2	2	T7	8.2	19.4	33.37	1.62	11.98	179	10.35	208.55	07.02
P2	4	T1	8.5	14	24.08	01.02	13.73	127	9.29	187.19	3.47
P2	4	T2	8.5	11.2	19.26	0.85	13.18	32	6.82	137.42	3.13
P2	4	T3	8.5	12	20.64	01.08	11.11	111	9.26	186.59	7
P2	4	T4	8.3	16	27.52	1.44	11.11	148	10.52	211.98	12.08
P2	4	T5	8.1	20	34.4	1.67	11.98	183	11.86	238.98	9.65
P2	4	T6	8.3	20.4	35.09	1.44	14.17	131	10.22	205.93	6.43
P2	4	T7	8.4	18.7	32.16	1.46	12.81	128	9.29	187.19	6.61
P2	6	T1	8.5	14.9	25.63	1.23	12.11	130	10.24	206.34	5.89
P2	6	T2	8.5	12	20.64	0.95	12.63	61	10.75	216.61	8.48
P2	6	T3	8.6	8.6	14.79	0.87	9.89	70	8.62	173.69	6.55
P2	6	T4	8.4	14.4	24.77	01.03	13.98	111	11.36	228.9	11
P2	6	T5	8.3	17.4	29.93	1.35	12.89	178	11.71	235.96	10.97
P2	6	T6	8.1	25.6	44.03	2.25	11.38	163	12.16	245.02	7.71
P2	6	T7	8.5	16	27.52	01.06	15.09	144	9.58	193.04	4.65

K2O (mg/kg)	SODIUM	Na2O (mg/kg)	CEC
175.21	0.66	20.46	81
130.47	0.37	11.47	73
458.28	1.31	40.61	125
272.71	0.45	13.95	91
296.26	0.89	27.59	107
292.49	0.53	16.43	109
148.84	0.5	15.5	99
199.23	0.6	18.6	98
141.3	0.5	15.5	86
336.77	0.94	29.14	99
277.89	0.72	22.32	109
249.63	0.6	18.6	111
276.95	0.86	26.66	145
156.84	0.78	24.18	112
142.71	0.54	16.74	84
188.87	0.39	12.09	77
534.59	0.7	21.7	108
195.47	01.05	32.55	88
212.42	0.62	19.22	129
260.93	0.73	22.63	107
198.29	1	31	209
238.33	0.67	20.77	126
451.22	0.48	14.88	136
592.99	0.92	28.52	148
358.43	0.63	19.53	132
404.12	0.82	25.42	151
361.26	0.6	18.6	120
471.94	0.69	21.39	113
370.68	0.63	19.53	129
526.58	0.66	20.46	126
592.52	01.09	33.79	131
318.87	0.51	15.81	106
327.82	0.75	23.25	138
252.93	0.7	21.7	142
357.96	0.67	20.77	128
506.8	0.7	21.7	129
233.62	0.63	19.53	112
349.01	0.83	25.73	164
154.02	0.67	20.77	83
228.44	0.77	23.87	159
316.98	0.55	17.05	126
455.93	0.56	17.36	121
378.68	0.82	25.42	128

266.59	0.41	12.71	100
330.64	0.57	17.67	125
163.44	1	31	87
147.42	0.95	29.45	138
329.7	0.89	27.59	105
568.97	0.65	20.15	94
454.52	0.77	23.87	131
302.85	1	31	117
311.33	0.46	14.26	130
277.42	0.79	24.49	111
399.41	0.68	21.08	131
308.51	0.6	18.6	133
518.1	0.54	16.74	125
516.69	0.59	18.29	140
363.14	1.27	39.37	149
219.02	0.53	16.43	96

Name	Description
Field	Study site where the sample was taken, P1 is the Roujan vineyard and P2 is the Combaillaux vir
Interrow	Index of the interrow sampled
Transect	Position along the transect sampled, T1 is upslope of the field

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Appendix B. Mean E/S ratio (number of seedlings counted divided by the surface of one sample) values and standard deviation for each study site (P1 : Roujan study site, P2 : Combaillaux study site) and each dispersal mode considered, separated by the zones accounted for in the statistical analyses. Combined effect of dispersal mode and zone sampled was tested by performing an ANOVA on a generalized linear model for each site separately, and differences between zones and between dispersal modes were tested using Tukey tests. Significant differences between dispersal modes are represented by different lowercase letters, and differences between zones are represented by different uppercase letters.

	Anemochory		Barochory		Hydrochory		Zoochory	
	P1	P2	P1	P2	P1	P2	P1	P2
Study site	34.6 +/- 23.1 ^a	32.5 +/- 32 ^a	128 +/- 258 ^b	133 +/- 218 ^c	34 +/- 42.5 ^a	87.3 +/- 102 ^b	28.9 +/- 28.4 ^a	37.2 +/- 34.5 ^a
Field	22.0 +/- 12.84 ^A	20.96 +/- 17.24 ^{Ab}	43.95 +/- 33.64 ^A	160.04 +/- 282.66 ^{Aa}	24.53 +/- 14.04	115.79 +/- 123.27 ^{Aa}	23.6 +/- 18.2	26.56 +/- 29.22 ^{Ab}
Field edge	38.95 +/- 28.14 ^{Bac}	28.93 +/- 24.44 ^{Ba}	248.64 +/- 445.41 ^{Bb}	122.72 +/- 135.7 ^{Bb}	51.78 +/- 78.51 ^a	49.47 +/- 60.88 ^{Aa}	39.76 +/- 44.81 ^a	38.02 +/- 29.8 ^{Ba}
Ditch	47.71 +/- 20.93 ^{Ca}	77.5 +/- 43.88 ^C	150.69 +/- 166.67 ^{Bb}	61.53 +/- 44.28 ^{AB}	33.23 +/- 13.85 ^a	75.36 +/- 43.86 ^B	28.77 +/- 20.97 ^a	74.47 +/- 40.12 ^C