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► **To cite this version:**

M. Neyret, Anneke de Rouw, Nathalie Colbach, Henri Robain, B. Soulléuth, et al.. Year-to-year crop shifts promote weed diversity in tropical permanent rainfed cultivation. *Agriculture, Ecosystems & Environment*, 2020, 301, 11 p. + 9 p. 10.1016/j.agee.2020.107023 . hal-02912968

**HAL Id: hal-02912968**

**<https://hal.science/hal-02912968>**

Submitted on 22 Aug 2022

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# Year-to-year crop shifts promote weed diversity in tropical permanent rainfed cultivation

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## Abstract

In the past decades, the expansion and modernisation of agriculture in the mountainous areas of Southeast Asia has had severe impacts on biodiversity, as the once species-rich forests were turned into homogeneous fields receiving ample external inputs. A common feature of permanent cropping with annual crops is the frequent change of crop choice, depending on market opportunities or other motives. However, the precise effect of crop shifts on weeds in tropical areas is largely unknown. In this study, we investigated the short-term effect of crop sequences on the diversity of weed communities in smallholder fields in Northern Thailand. Crop choices were upland rice, maize, fallow and young tree plantations with or without intercrop. We counted the number of crop shifts and the number of crops involved during a 3-years period preceding weed sampling. We showed that the number of crop shifts did not affect weed density and biomass. However, herbaceous species number and diversity (measured as Shannon index) increased by 36% and 46% respectively, while herbaceous species dominance decreased by 38%, in fields with yearly crop shifts compared to fields with no shifts in the previous three years. The effect of a particular crop on diversity, or the effect of intercropping with young trees, was weaker. It was likely due to the more variable resources (especially light) in fields with two crop shifts, allowing species with different niches to co-exist. Crop type and frequent crop shifts did not affect shrub and tree species number,

26 diversity or dominance. Some species were strongly associated with fields with no crop shift in the  
27 sequence (e.g. the tree *Antidesma velutinsum*) or to fields with two crop shifts in the sequence (e.g.  
28 the herb *Centella asiatica*, the C<sub>4</sub> grass *Digitaria radicata*). Overall, this study showed that in this  
29 agronomical system, maintaining yearly crop shifts does not significantly affect weed abundance,  
30 but supports in-field plant species diversity, which is likely to impact the services provisioned by  
31 tropical mountainous agro-ecosystems.

## 32 **Highlights**

- 33 • Frequent crop shifts in a crop sequence increased weed richness and diversity.
- 34 • Crop shifts had a stronger effect on weed richness and diversity than the current crop.
- 35 • The number of crop shifts did not affect weed biomass and density.

## 36 **Keywords**

37 Crop rotation; Southeast Asia; weeds community; smallholder; Thailand; rainfed rice; rubber tree  
38 intercropping; maize

## 39 **1. Introduction**

40 The growing use of pesticides and fertilisers and the decrease of crop diversity associated with the  
41 modernisation of agriculture have led to a worldwide decrease of in-field biodiversity, soil quality  
42 and organic matter content, and an acceleration of surface water eutrophication (Tilman, 2001;  
43 Tschardtke et al., 2005). In temperate areas, agricultural intensification has been shown to strongly  
44 affect weed communities, by favouring species that are more competitive and mimic the main crop  
45 (Fried et al., 2010, 2012, 2015) and overall by decreasing in-field weed diversity and abundance  
46 (Squire et al., 2000; Hyvönen and Salonen, 2002; Baessler and Klotz, 2006; Fried et al., 2009;  
47 Hyvönen et al., 2011).

48 Yet, multiple ecosystem services depend on the maintenance of weed diversity (Matson et al.,  
49 1997; Tschardtke et al., 2005). Diverse plant communities are indicative of the wider sustainability  
50 and resistance to stress of the cropping system (Chen et al., 2004; Storkey and Neve, 2018). They  
51 provide food sources for biodiversity at higher trophic levels during extended periods (Marshall et  
52 al., 2003; Petit et al., 2011; Edesi et al., 2012) and promote large and rich populations of pollinators  
53 necessary to the cultivation of arthropod-pollinated crops (Bàrberi et al., 2010). Plant cover is also a

54 major element of soil conservation by favouring infiltration, enhancing soil structure and organic  
55 carbon stocks (Durán Zuazo and Pleguezuelo, 2008). Contrasted plant traits have been shown to  
56 protect soil in various ways: the root density and the proportion of fine roots limit surface erosion  
57 (Burylo et al., 2012a, 2012b) while deeper roots stabilise slopes (Stokes et al., 2008). As a result,  
58 diverse weed communities enhance erosion mitigation: diverse root growth forms, for instance,  
59 have been shown to increase soil protection (Beierkuhnlein and Jentsch, 2004). Weeds also provide  
60 other key services such as pest control (Crowder and Jabbour, 2014), water filtration or nutrient  
61 cycling (Gholamhoseini et al., 2013a, 2013b; Yagioka et al., 2015), which are severely threatened by  
62 current agricultural changes.

63 From the 1970s onward, population growth and rapid economic development led to the expansion  
64 of arable lands to the detriment of natural and semi-natural areas and to a quick increase in the use  
65 of herbicides and fertilisers (Rerkasem and Rerkasem, 1995; Rigg et al., 2012). The development of  
66 cash crops was associated with the disruption of traditionally diverse cropping systems (Rerkasem  
67 et al., 2009). In Southeast Asia, one of the hotspots of biodiversity worldwide, these changes have  
68 occurred at an unprecedented scale (Fox et al., 2014). A better understanding of the relationships  
69 between these changes in cropping practices and non-cultivated biodiversity is particularly critical  
70 in mountainous areas, where biodiversity has been strongly affected by the recent modernisation of  
71 farming practices (Rerkasem et al., 2009).

72 Crop rotation is the practice of growing different crops on the same land from year to year  
73 following a more or less fixed cycle. Besides their well-known positive effects on soil health and  
74 fertility (Watson et al., 2002), erosion mitigation (Morgan, 2005), and crop disease risk reduction  
75 (Colbach et al., 1994), crop rotations are also an important method of weed control, as they prevent  
76 the build-up of aggressive weed communities linked to cultivating the same crop over and over  
77 again (Liebman and Dyck, 1993, Radosevich et al., 1997, Doucet et al., 1999; Squire et al., 2000 ;  
78 Adler et al., 2006; Ulber et al., 2009; Allan et al., 2014; Gaba et al., 2014). Most of these studies  
79 investigated the effect of well-defined rotations (Cardina et al., 2002; Nikolić et al., 2018; Shahzad et  
80 al., 2016) such as the common maize-soybean-wheat (Doucet et al., 1999) on weed communities  
81 and crop yield. A few studies have also proposed various metrics to define crop rotations, such as  
82 the proportion of a focus crop in the rotation. But the idea that crop rotations follow a fixed pattern  
83 can be questioned (von Redwitz and Gerowitt, 2018). In Southeast Asia, the rainfed cultivation such  
84 as the system we studied does not follow predetermined patterns, but rather results from year-to-  
85 year decisions based on the current meteorological or socio-economic context. There is an element  
86 of randomness that may be linked to the choices of individual farmers. The effect of these crop

87 sequences on weed communities is unknown. It is urgent to investigate the weed diversity under  
88 any crop sequence, not only under the sequence of the rather standard and well-known crop  
89 rotations.

90 In this study, we determine the effect of crop sequences on the richness, diversity, biomass and  
91 density of weed communities in fifteen permanently cropped smallholder fields in mountainous  
92 Northern Thailand. We characterised the sequences using the number of crop shifts, and the  
93 number of crop types. We also aimed at identifying species that are indicators of fields with frequent  
94 crop shifts. We conducted weed sampling in the rainy season to collect additional information on  
95 agricultural practices and crop stand and in the dry season to collect information on the effect on  
96 weeds of post-harvest conditions such as water availability. We hypothesised that fields with  
97 frequent shifts would have more diverse and less abundant weed communities, especially in the dry  
98 season when the effect of the most recent crop is weaker, while weed biomass would be overall  
99 higher in the rainy season due to higher water availability.

## 100 **2. Material and Methods**

### 101 **2.1. Study site**

102 The study site was located in Huai Lang, Chiang Rai province, northern Thailand. The site is part of  
103 a wider project investigating the soil-water effects of land use transitions. The fields were located in  
104 and around two catchments, respectively dominated by annual cultivation or rubber tree  
105 plantations. An automatic weather station (Campbell BWS200) has been installed on-site since  
106 March 2015. The site is characterised by  $1300 \pm 200$  mm of annual rainfall, mostly falling during the  
107 rainy season (May to November). Mean annual temperature is  $24.5 \pm 0.4$  C, with daily temperatures  
108 ranging from 4.8 to 42.5 C. A detailed soil mapping showed that soils are Haplustalfs (Alfisols) and  
109 belong to three soil series (Tha li, Wang Saphung, and Muak Lek, based on Jumpa (2012)), mostly  
110 differentiated on depth and slope criteria. The soils were otherwise rather uniform, well drained  
111 and with clay to clay-loam texture.

112 Paddies (wet rice), maize fields and settlements occupied most of the flatlands but we focused our  
113 study the rain-fed fields of the hillslopes, which have typically steep slopes ranging from 27 % to 54  
114 % (median 40 %). The size of the study fields ranged from 0.64 ha to 2.6 ha (median 1.6 ha). On the  
115 hillslopes, maize (cash crop) and upland rice (subsistence crop) were grown in monoculture or as  
116 an intercrop between rows of young trees (most often immature rubber trees). Farmers prepared  
117 their fields between April and June and, with a few exceptions, they burnt crop residues before

118 seeding. In a given field, maize was grown for one, two or three consecutive years and rice only for  
119 one or two years. Upland rice was planted at the beginning of the rainy season (late May-June)  
120 whereas the planting period of maize was more flexible. Indeed, being a crop with a short growing  
121 season, maize could be sown later in the rainy season (from May and up to July) and benefited from  
122 the long growing season associated with the bimodality of the climate. Maize and rice were  
123 harvested during October and November, respectively. The steep slopes did not permit ploughing  
124 and the soil was mostly left undisturbed, except for occasional manual surface hoeing. The upland  
125 rice varieties in the study area were long-cycle landraces (i.e. locally adapted varieties), typically tall  
126 varieties with drooping leaves providing dense shadow. In contrast, the maize varieties were  
127 modern, short-cycle and herbicide-resistant improved varieties grown as a cash crop for animal  
128 feed. Rice was planted in hills with an average density of 130 000 hill/ha, which was common for  
129 landraces in the area. Maize was sown in densities of 31 000 hill/ha, with two plants per hill, which  
130 was in the low range of typical sowing densities (20 000 hill/ha to 80 000 hill/ha). In both maize  
131 and rice glyphosate was the most common herbicide, applied with rates ranging from 0.7 L/ha to 25  
132 L/ha (at 480 g/L) and often in combination with other herbicides such as paraquat or atrazine  
133 (Neyret et al., 2018). These values, displaying a surprisingly large range, were reported by farmers  
134 but could not be checked in the field. Herbicides were sprayed before or just after sowing in rice  
135 (May - June), and before sowing (April - May) and sometimes after emergence (July) in maize. Most  
136 farmers fertilised their field by applying 13 kg/ha to 130 kg/ha of fertiliser: usually urea (46-00)  
137 once a year, more rarely twice a year or in combination with ammonium sulphate (21-00) or NPK  
138 fertilizer (15-15-15).

139 Rubber (*Hevea brasiliensis*) is an important cash crop in the study area. The oldest plantations  
140 were planted at the beginning of the 2000s, and the expansion of rubber trees is ongoing. Saplings of  
141 rubber trees are planted on the slopes (approx. 500-550 trees/ha) and commonly intercropped  
142 with maize or upland rice during 4 - 5 years when young allowing farmers to improve their income.  
143 Intercropping of maize and upland rice with longan fruit trees (*Dimocarpus longan*) is also common.  
144 Longan is planted in low densities (approx. 300 trees/ha).

## 145 **2.2. Sampling protocol**

146 In March 2016, we selected 15 fields (five maize fields, five upland rice fields, five young rubber  
147 trees plantations with maize intercrop). We chose field locations in order to avoid spatial clustering  
148 of similar crops. This was done by selecting distinct sectors with at least 2-3 different crop types  
149 within a few hundred meters each. In each field, we delimited a 100-m<sup>2</sup> area in a section

150 representative of the whole field (i.e. avoiding field edges and large terrain irregularities). We then  
151 divided this area into a regular grid of ten by ten 1-m<sup>2</sup> subplots and randomly drew 5 numbers  
152 between 1 and 100, which determined the position of five 1-m<sup>2</sup> subplots in the grid. We conducted  
153 complete botanical inventories (e.g. individual plant counts and identification) in these subplots. We  
154 also collected the aboveground biomass of all living herbaceous weeds, shrubs and trees (thus  
155 excluding crop biomass); it was stored in paper bags and dried at 50 °C for 48 h before weighting.  
156 Biomass measurements were then averaged for each field. As resprouting trees and shrubs were  
157 less abundant than herbaceous species, we also counted and identified all trees and shrubs in the  
158 100-m<sup>2</sup> areas. Both herbaceous and shrub/tree densities exclude crops, and were then converted to  
159 the average number of plants per square meter for each 100-m<sup>2</sup> area.

160 In total, this protocol was maintained in the same fields (but in different subplots) during three  
161 years. Sampling was conducted three times in the dry season (in March 2016, 2017 and 2018,  
162 before field preparation); and twice in the rainy season (October 2016 and November 2017, just  
163 after the harvest). Sometimes the crop was not fully mature and we sampled fields shortly before  
164 harvest - and thus did not collect data on yield. In the rainy season soil moisture was on average 2 to  
165 3 times higher than in the dry season (Neyret, 2019). Samplings were conducted at least two (rainy  
166 season) or seven (dry season) months after the last herbicide application.

### 167 **2.3. Diversity indices**

168 We used multiple descriptors of weed communities that provided complementary information  
169 (Table 1). Plant biomass and density provided information on the potential aggressiveness of weed  
170 communities towards the crop. The number of weed species is a simple measure of plant richness,  
171 which we complemented by diversity and dominance indices – describing respectively the diversity  
172 of the whole community (Shannon index, noted H') and the strength of the dominance by the main  
173 species (Berger-Parker index, noted D). Diversity and dominance are important indicators of the  
174 resistance and the resilience of an ecosystem, as more diverse communities are likely to be more  
175 stable and resilient (McCann, 2000).

176 We ranked the species according to a Relative Importance index RI (e.g. Cardina et al., 2002),  
177 adapted from the Importance Value Index (which also takes into account biomass or basal area) to  
178 distinguish between the most common, intermediate and rare species.

$$179 \quad RI_i = \frac{1}{2}(f_i + p_i)$$

180

181 RI ranged from 0 to 1 and was calculated for each species  $i$  as the average of its relative frequency  
182 ( $f_i$ , number of plots where species  $i$  was found divided by the total number of plots) and relative  
183 abundance ( $p_i$ , number of individuals in species  $i$  divided by the total number of individuals). □

#### 184 **2.4. Quantification of crop sequence variability**

185 Information on land uses in 2013, 2014, 2015 was obtained during the first sampling in 2016 from  
186 interviews with landowners and from direct observation of crop residues. Hence, we obtained a  
187 five-year crop sequence for each field, which we divided into three three-year sequences (Fig. 1).

188 We quantified crop sequence in two ways, (1) number of crop shifts over three years, (2) total  
189 number of crops involved in the three years. We described the crop using two variables, (1) annual  
190 crop type - either maize, upland rice, or no crop i.e. fallow - and (2) young trees intercropping with  
191 annual crop or annual crop solo (Table 2). These trees were either rubber or longan trees.

192 For instance, maize-maize-maize sequence counts as no shifts and one crop type; maize-maize-rice  
193 counts as one shift and two crop types; maize-rice-maize counts as two shifts and two crop types;  
194 and maize-rice-fallow counts as two shifts and three crop types. For some fields, we were able to  
195 describe crop history only from 2014 onwards, in which case the first sequence was not used (Table  
196 3).

197 Maize was the most represented annual crop in the dataset. In order to validate our main results  
198 regarding the impact of crop shifts irrespective of the identity of the current crop, all analyses were  
199 conducted twice: i/ including all available data; and ii/ including only fields with maize as the  
200 current annual crop (i.e. maize monoculture or young tree plantations with maize intercrop). For  
201 these analyses, we compared maize fields with no crop shift ( $n = 17$ ) or two crop shifts ( $n = 7$ )  
202 because there were not enough maize fields with only one shift ( $n = 3$ ).

#### 203 **2.5. Statistical analyses**

204 All analyses were conducted using R (R Core Team, 2018). We built models for each weed  
205 community characteristic described in Table 1 as a response variable. We used linear mixed models  
206 (functions *lmer* and *lme*, packages *lme4* (Bates et al., 2014) and *nlme* (Pinheiro et al., 2018) in R).  
207 Each model included as explanatory variables: the annual crop type, the presence of trees, and a  
208 spatial covariate (see below), and the temporal crop variability and its interaction with sampling  
209 season. The temporal crop variability was measured either as the number of crop shifts (levels: 0, 1  
210 or 2) or the total number of crops involved (1, 2 or 3) in the three preceding sampling seasons (2 df,  
211 Degrees of freedom).



212 Spatial autocorrelation was also included in the model, fitted with the *lme* function, as an  
213 exponential correlation structure (function *corSpatial*). Beforehand we scaled the easting and  
214 northing coordinates of each field and added a small jitter (normal noise, mean of 0 and standard  
215 deviation of 0.001) because the function cannot handle duplicate coordinates. Other forms of spatial  
216 autocorrelation (gaussian, linear, spherical) were tested but model AIC were similar. All significance  
217 values and estimates are extracted from these models. However, to provide estimates of partial  $R^2$   
218 for each single variable (function *r2beta*, package *r2glmm*, Kenward Roger method, Jaeger (2017))  
219 we had to use model fitted with the *lmer* function (i.e. without spatial autocorrelation) due to  
220 package compatibility issues. As the autocovariates were not significant, this was unlikely to  
221 strongly affect the  $R^2$ .

222 Besides, the treatment of interest (number of crop shifts) was not independent of the field itself or  
223 the crop type. Indeed, we conducted botanical inventories repeatedly in the same fields and the  
224 number of crop shifts in one site was not independent from one year to another: a field with two  
225 crop shifts (or respectively zero) on a given year would necessarily have at least (resp. at most) one  
226 shift the next year. In order to take into account this non-independence, we used field-level random  
227 effects in the models. Plant densities (always strictly positive) were log-transformed, and biomasses  
228 square-root-transformed, to ensure normality of the residuals. We conducted pairwise comparisons  
229 between each level of crop temporal variability (e.g., for the number of crop shifts, 0 v. 1, 0 v. 2 and 1  
230 v. 2 shifts; and for the number of crop types, 1 v. 2, 1 v. 3, and 2 v. 3 crop types) while keeping the  
231 other explanatory variables constant (*emmeans* function, package *emmeans*, Lenth (2018)). The  
232 significance of each variable in the full model was assessed using Anova type II or III tests (function  
233 *Anova*, package *car*, Fox et al. (2011)): thus, the effect of each variable was tested "after", or  
234 "controlling for" the other fixed effects present in the model.

235 Models including only maize fields were also mixed models including spatial autocovariates, and  
236 the explanatory variables were the same (except for the annual crop variable, which was not  
237 included).

238 In additional sensitivity analyses, the year was also included as a fixed effect in the models. The  
239 models were then selected based on AIC. The results from these analyses were consistent with our  
240 main results and are not presented for concision.

## 241 **2.6. Indicator species analysis**

242 Our last objective was to determine whether certain species were specifically associated with  
243 either high or low frequency of crop shifts. In this regard, we identified groups of indicator species

244 related to each number of crop shifts. As proposed by Cáceres and Legendre (2009), indicator  
245 species are species that can be used as ecological indicators of environmental and ecological  
246 conditions. Their association to a given environment (here, over periods of three years, the number  
247 of crops or number of shifts) is based on the specificity and the fidelity of the species as an indicator  
248 of the environmental group (i.e. here, fields with a given frequency of crop shifts). We used the  
249 *indicspecies* package (function *multipatt*, *IndVal.g* method, Cáceres and Legendre (2009)).

## 250 **3. Results**

### 251 **3.1. Diversification of crop sequences**

252 From 2014 to 2018, we observed a total of 22 distinct crop sequences (Fig. 2), and an increasing  
253 diversity in crop sequences with time. In the period 2013-2015 five different sequences occurred, in  
254 the period 2015-2017 this increased to eleven (Fig 2). For instance, continuous maize cultivation  
255 (i.e. the sequence maize - maize - maize) was only observed in the period 2015-2017. Instead,  
256 fallows appeared and young rubber tree plantations were intercropped with rice or maize during  
257 four to five years before the shade from the canopy prevented further intercropping.

258 The number of crop shifts was not independent of crop type: maize fields were more often  
259 associated with continuous cropping (no shift) compared to upland rice or fallows which were  
260 always subject to crop shifts after 1 or 2 years ( $\chi^2$  test,  $P < 10\%$ ). Some farmers reported that the  
261 decision to grow maize (cash crop) or rice (subsistence crop) depended on both market and familial  
262 factors: a family running out of rice would be more likely to grow rice the next year, while the  
263 market price of maize might determine the planting of maize fields. This decision was also likely to  
264 depend on the start of the rainy season, as maize has a shorter cycle and needs therefore only part  
265 of the rainy season to complete its growth.

### 266 **3.2. Plant richness**

267 We found a total of 56 herbaceous species (52 identified at least to genus level), and 79 woody  
268 species (all identified) (Table S1). Fields in the dry and rainy season were equally species-rich, with  
269 6 to 26 (median 18) species per field in the dry season and 7 to 32 (median 18) species per field in  
270 the rainy season ( $P = 0.2$ , after controlling for crop type and crop shifts). We identified three groups  
271 of species based on breaks in the Relative Importance index bar plot (Fig. 3). Three herbaceous  
272 weeds (*Ageratum conyzoides* and *Conyza sumatrensis*, Asteraceae and *Mitracarpus hirtus*, Rubiaceae)

273 had a Relative Importance Index  $> 0.4$ , indicating that they were both very frequent and abundant.  
274 We identified 9 intermediate species with a RI comprised between 0.2 and 0.4. The least common  
275 species had a RI lower than 0.1 and comprised most shrub and tree species; among them, 43 species  
276 had a RI  $< 0.01$ .

277 Figure 4 shows an increase in species number among herbaceous species with more frequent crop  
278 shifts, particularly in the dry season. In fields where the crop changed every year, an average of 13  
279 herbaceous species were recorded in the third year. This is a 36 % increase ( $P = 0.03$ ), compared to  
280 fields where three years the same crop was cultivated, where only 8.3 herbaceous species were  
281 recorded on the third year (Fig. 4). This effect was stronger than that of the crop type itself (based  
282 on partial  $R^2$ , Table 4). The richness of trees and shrubs species or of the overall community was not  
283 affected by the number of crop shifts either during the dry or the rainy season (Fig. 4, Table 4).  
284 When considering the number of crop types instead of the number of crop shifts, herbaceous  
285 species number also tended to increase with the number of crop types but the relationship was not  
286 significant.

287 Similarly, maize monocultures tended to have lower herbaceous species number than fields with  
288 maize as the current annual crop (i.e. maize fields or young tree plantations intercropped with  
289 maize) with two shifts in the three previous years. It was significant in the rainy season ( $P = 0.02$ )  
290 but only a trend in the dry season ( $P = 0.07$ , Table S3, Fig. S1).

### 291 **3.3. Plant biomass and density**

292 Plant biomass (square root-transformed) and density (log-transformed) did not vary with the  
293 number of crop shifts nor the number of crop types ( $P > 0.1$ , Table 4, S2). When controlling for the  
294 number of shifts, annual crop type and the presence of trees, weed communities had lower densities  
295 ( $228 \text{ plant/m}^2$ ) and slightly higher biomass ( $70.2 \text{ g/m}^2$ ) in the dry compared to the rainy season  
296 (density of  $412 \text{ plant/m}^2$  ( $P = 0.01$ ) and biomass of  $44 \text{ g/m}^2$  (N.S.  $P = 0.08$ )).

297 Maize monocultures had significantly lower plant biomass ( $3.2 \text{ g/m}^2$  on average) and plant density  
298 ( $403 \text{ plant/m}^2$ ) than maize fields with two shifts in the three previous years (respectively  $88 \text{ g/m}^2$ ,  
299  $P = 0.01$ ; and  $1636 \text{ plant/m}^2$ ;  $P = 0.03$ ) in the rainy season. The difference was not significant in the  
300 dry season ( $P > 0.3$ , Table S3).

### 301 **3.4. Plant diversity**

302 Herbaceous weed communities were more diverse when the number of crop shifts increased,  
303 particularly in the dry season. There, the Shannon index  $H'$  increased by 46% from fields with no

304 crop shift (0.7 on average) to in fields with two crop shifts (1.3,  $P = 0.009$ , Table 4). This effect was  
305 stronger than that of the crop type itself (based on partial  $R^2$ , Table 4). The same trend was  
306 observed for diversity in the total community (shrubs/trees included,  $P = 0.04$ ) but not for  
307 shrub/tree communities only ( $P > 0.8$ ). Herbaceous plant communities were generally more diverse  
308 in the dry season ( $H' = 0.98$ ) compared to rainy season ( $H' = 0.78$ ,  $P = 0.03$ ).

309 All communities were dominated by the two most abundant species – usually *A. conyzoides*  
310 (dominant in 57% of the fields) followed by *C. sumatrensis* (22% of the fields) -, yet this dominance  
311 was weaker when the number of crop shifts increased. Indeed, in fields with no shift, the dominance  
312 (Berger-Parker index,  $D$ ) was 0.8 on average, which indicates that the most abundant species  
313 represented 80 % of all individuals. Conversely, dominance index decreased by 38% (to  $D = 0.5$  on  
314 average) in fields with two crop shifts ( $P = 0.03$ , Table 4). Similar trends for diversity and  
315 dominance were observed when considering the number of crops (Table S2).

316 When controlling for the crop shifts, crop type and the presence of trees, dominance of herbaceous  
317 species, but not of shrubs and trees was significantly higher in the rainy ( $D = 0.7$ ) than the dry  
318 season ( $D = 0.6$ ,  $P < 0.05$ , data not shown). This can be explained by the declining numbers of the  
319 two dominant weeds *A. conyzoides* and *Conyza sumatrensis*, both annual species. Annual species  
320 tend to end their life cycle in the dry season, modifying dominance and diversity. This was not  
321 observed in woody species because they are all perennials. Conversely, Shannon index was higher in  
322 the dry ( $H' = 0.98$ ) compared to rainy season ( $H' = 0.78$ ,  $P = 0.03$ ) for herbaceous species; it was also  
323 significant for all species but not for shrub and tree species (data not shown).

324 Consistently with the results considering all crop types, the diversity of the total community in the  
325 dry season was lower in maize monocultures ( $H' = 1.1$ ) than in maize fields with two shifts ( $H' = 1.6$ ,  
326  $P = 0.01$ , Table S3). Diversity for the total community followed the same trend as for herbaceous  
327 species only, probably because the woody fraction was altogether relatively small in maize  
328 monoculture. Dominance did not vary significantly between maize monocultures and maize with  
329 two shifts.

### 330 **3.5. Indicator species**

331 We found that 12 species were indicators of a precise number of crop shifts, or a range of crop  
332 shifts, in the three years preceding sampling (Table 5). For example, *Digitaria radicata* (annual,  
333 creeping C4 grass) and *Centella asiatica* (perennial, creeping herb) were strongly associated to fields  
334 with two shifts while the shade-tolerant fern *Thelopterys subelatus* was a good indicator of fields  
335 with either one or two crop shifts in the previous three years. Conversely, *Antidesma velutinsum*, a

336 tree, *Streblus asper*, a shrub and *Tournefortia sp.*, a liana, were found mostly in continuous cropping,  
337 with no shifts over the previous three years.

## 338 **4. Discussion**

### 339 **4.1. Crop sequence variability**

340 In northern Thailand farmers often grow maize for several consecutive years, with occasionally  
341 upland rice to break the maize monoculture. Conversely, upland rice is only cultivated for 1 or 2  
342 consecutive years. Intercropping of upland rice and maize with young rubber trees whose canopy is  
343 still open enough or with longan saplings is another option for farmers. The farmers' motives for  
344 crop shifts and intercropping were difficult to apprehend and impossible to verify. However, we can  
345 distinguish between socio-economic reasons and ecological-technical ones.

346 Socio-economic motives include market prices and labour availability. For instance, the  
347 persistently low market price for rubber since 2011 induces farmers to plant fruit trees (longan)  
348 instead of rubber trees. Labour demand in upland rice is more important than in maize, yet rice  
349 requires less modern inputs compared to maize, e.g. hybrid seed, frequent herbicide spraying. More  
350 interesting, because linked to weed control strategies, are the ecological and technical motives for  
351 crop sequences. Weed infestation usually prevents cultivating rice more than 2-3 years in a row  
352 while maize as a crop is much more resistant to weeds (Sankaran and de Datta, 1986). Moreover,  
353 the herbicide-resistant maize varieties allow the continuing use of herbicides later in the season. In  
354 the study area weeds do not seem to limit the continuous cultivation of maize, however, a growing  
355 built-up of aggressive weeds could compromise a shift to upland rice. For instance, heavily infested  
356 fields in Laos no longer support upland rice (Dupin *et al*, 2009). The local bimodal rainfall  
357 distribution has a long rainy season but is subject to intermittent dry spells, which could lead  
358 farmers to favour maize over upland rice. Indeed, sowing and harvest dates of the traditional long-  
359 cycle upland rice varieties cannot be modified, while the short-cycle hybrid maize is more flexible:  
360 for instance, we observed both harvested and immature maize fields during our October 2016  
361 sampling. The reason for early or late planting could be to avoid drought. A second advantage of  
362 maize is that the hill density can be reduced to adjust to water availability: low density planting  
363 provides more opportunities for weeds to grow, but weeds can be controlled by late herbicide  
364 spraying. In upland rice, hill density is high and cannot be modified without compromising the  
365 weed-competitiveness of the leafy, high stature varieties.

366 This difference between rice and maize cultivation led to the emergence of two groups of crop  
367 sequences among the fields we investigated. One consisted of continuous maize cultivation (either  
368 continuous maize monoculture or intercrop between tree rows) and the other with alternating  
369 cultivation of maize and rice. Neyret *et al.* (2018) reported higher richness and greater diversity of  
370 weed communities in upland rice than in maize. A similar result is demonstrated here, in crop  
371 sequences containing upland rice and in sequences of only maize. Differences in cultivation and  
372 weeding practices among crops are at least partly responsible for the crop-effect in weed  
373 communities (Neyret et al., 2018). This leads to variability in community composition from year to  
374 year and thus to the increase of weed richness with the number of crop shifts. Thus, while the crop  
375 type effect and the “number of crop shifts” effect are partly confounded in this study, we tried to  
376 separate the two effects, i.e. by (1) including the effect of annual crop type and the presence of trees  
377 in the models, and (2) controlling for crop type before measuring the effect of the number of shifts.  
378 Besides, the positive effect of crop shifts on weed richness was at least partly supported when  
379 considering only maize fields, i.e. when removing any possible confusion with the annual crop  
380 currently grown in the field. Thus, while crop type was very likely to affect the richness, diversity  
381 and abundance of weeds in this trial, we showed that the number of shifts had an effect  
382 independently from crop type.

#### 383 **4.2. Crop shifts increase herbaceous species number and diversity**

384 Our finding that plant diversity increases with shift frequency is also consistent with the literature.  
385 Previous studies, mostly in temperate areas, indeed found that increasing the inter-annual  
386 variability of land use had a positive effect on weed richness and diversity (Liebman and Dyck,  
387 1993; Doucet et al., 1999; Squire et al., 2000; Ulber et al., 2009). For instance, Allan et al. (2014)  
388 showed that in grasslands, weed richness (and especially rare plants richness) increased with the  
389 temporal heterogeneity of fertilisation, mowing and grazing intensity, independently of the level of  
390 intensity itself. Using a simulation approach, Bürger et al. (2015) showed that while tillage was the  
391 main factor affecting weed diversity, the simplification of crop rotations also reduced biodiversity,  
392 especially in regions already harbouring low diversities.

393 In addition, our study showed that the effect of the number of crop shifts on herbaceous species  
394 number and diversity was stronger than that of crop type, contrarily to previous results (Bàrberi et  
395 al., 1997; Smith and Gross, 2007). The outcome of studies investigating the effects of temporal  
396 diversity on plants depends on the timescale of the study. Such effects are likely to be noticeable  
397 only when looking at the total weed flora within a field, by looking either at the seedbank or at the

398 flora over multiple years, as opposed to looking at the flora within a single year only (Dessaint et al.,  
399 1997). Altogether, this suggests that in the long-term, the severely degrading effect on biodiversity  
400 of some crops could be offset by annual rotations with more biodiversity-friendly land uses.  
401 Additional studies of similar agro-ecosystems investigating the effect of longer-term crop rotations  
402 could thus provide further confirmation of our results.

### 403 **4.3. Species associated with high shift frequency**

404 Although no species were entirely restricted to a given frequency of crop shifts, we were able to  
405 show that some species were significantly associated to either frequently shifting fields or  
406 continuous crops. The three dominant herbaceous species – *Ageratum conyzoides*, *Mitracarpus*  
407 *hirtus* and *Conyza sumatrensis*) were ubiquitous, and thus not associated to any particular crop. All  
408 species associated with fields with zero shift or one to two shifts were tree species, while the two  
409 species most significantly associated with fields with two shifts (*Digitaria radicata* and *Centella*  
410 *asiatica*) were herbaceous annuals. Besides, contrarily to herbaceous species, trees and shrubs  
411 richness and diversity did not respond to changes in the number of crop shifts or the number of land  
412 use types. This suggests a weaker response of trees and shrubs to year-to-year shifts, compared to  
413 herbaceous species, which grow and reproduce more quickly. Indeed, perennial species (including a  
414 few of the herbaceous species, but all shrub and tree species) have more underground reserves  
415 from which they can directly regrow (Raunkiaer, 1934). This makes them less dependent on local  
416 conditions and farming practices to establish in a given field.

### 417 **4.4. Seasonal effect on weeds richness and abundance**

418 We showed that although species number did not vary significantly with season, there was a  
419 strong decrease in plant biomass, but increase in plant density in the rainy season compared to the  
420 dry season. Fewer yet larger individual plants in the dry season than in the rainy season can be  
421 explained by a combination of at least three factors. The life cycle of annual weeds runs with the  
422 rainy season so their life cycle naturally ends in the dry season, reducing density. Secondly, the dry  
423 season, for its lack of surface soil moisture, is less suitable than the rainy season for new  
424 emergences; instead, well-established individuals can expand in the dry season, their roots  
425 exploring moisture in the deeper soil layers. Finally, the fields sampled in the dry season had not  
426 experienced weed control for at least six months, allowing for self-thinning among seedlings and the  
427 outgrow of the more vigorous individuals.

428 Most of the seedlings found in the rainy season belonged to the three dominant species, which also  
429 explains the decrease in species diversity, and the increase in the dominance index. *A. conyzoides* in  
430 particular has a very effective reproduction rate, producing numerous seeds with high germination  
431 rates (Kohli et al., 2006; Hao et al., 2009). This dominance by the main species in the rainy season  
432 was likely to explain the strongest response to crop shifts on species number in the dry compared to  
433 rainy season.

#### 434 **4.5. Resource and disturbance variability**

435 Gaba et al. (2014) identified two main gradients driving the abundance and diversity of weeds in  
436 crop rotations. On the one hand, the resource variability gradient represents the temporal  
437 variability of resource availability in the field, which is expected to increase weed diversity through  
438 niche diversification. On the other hand, the disturbance gradient represents the type and frequency  
439 of disturbance, which is expected to increase mortality rates and to decrease weed abundance.

440 Contrarily to our expectations, we did not detect a change in weed biomass or weed density with  
441 crop shifts. This was probably due to the fact that fields with frequent shifts did not necessarily have  
442 a higher variability of disturbance types and timing, which is expected to be the main driver of the  
443 changes in weed abundance (Gaba et al., 2014). Maize and rice fields had relatively similar soil  
444 preparation as well as fertilisation rates: thus, the type and timing of disturbance were unlikely to  
445 differ among fields (except for fallows). While in this trial we did not have data on crop yield, the  
446 experiment was farmer-managed, thus weed control was assumed sufficient in achieving an  
447 acceptable yield. Additional measures of yield and crop biomass would be needed to confirm  
448 whether the frequency of crop shifts affects the actual aggressiveness of weed communities towards  
449 the crop.

450 In terms of resource variability, rice and maize created different light conditions, which is known  
451 to be an important determinant of weed growth (Holt, 1995): while rice grows very densely, quickly  
452 covering the ground and limiting weed growth, maize (planted at relatively low density in the study  
453 system) leaves most of the soil bare and triggers the germination of photosensitive species. Many  
454 common tropical weed seeds require full sunlight to germinate (example *A. conyzoides* and *C.*  
455 *sumatrensis*), while other prefer light shade (*Chromolaena odorata*) (Garwood, 1989; de Rouw et al.,  
456 2013). Thus, in fields with frequent shifts, the reproduction rates of very competitive, heliophilous  
457 species with high seed production are regularly lowered by less favourable conditions. This creates  
458 opportunities for new species to germinate from the seedbank or to establish from neighbour  
459 communities, and explains the lower dominance index in fields with frequent shifts. Frequent shifts



460 thus prevent the selection of species functionally close to the crop (Liebman and Dyck, 1993; Smith  
461 et al., 2010).

462 Sites with permanent annual cropping have large seed banks, between 5000 and 10 000 viable  
463 seeds/m<sup>2</sup> (Garwood, 1989). In Laos, soil seed banks were found similar across upland rice sites, in  
464 density and composition, but weed species abundances in the cultivated fields were not correlated  
465 with densities in the seed bank. These results indicate that emergence during the cultivation period  
466 reflected the local growing conditions far more than their availability in the seed bank (de Rouw et  
467 al., 2013). In our study system, rice and maize residues are likely to create different humidity  
468 conditions, which could favour the germination of different fractions of the seedbank. Rice and  
469 maize also had different sowing and harvesting times, which have been shown to be major  
470 determinants of the functional composition of weed communities (Gunton et al., 2011). For instance,  
471 maize has a much shorter growing period, which leaves the fields almost fallow-like with dry maize  
472 stalks during a large part of the year. The later application of herbicides in maize (e.g. after  
473 germination), repeated in maize fields with no shifts, might also have led to the selection of species  
474 able to recover quickly after spraying, such as *A. conyzoides*. Thus, crops changing from year to year  
475 provide variable germinating and growing conditions for weeds, and a selection of different species  
476 from one season to another. This allows the maintenance of diverse communities over time by  
477 allowing species with different responses to the environment to coexist stably in different niches  
478 (Allan et al., 2014; Gaba et al., 2014).

## 479 **6. Conclusion**

480 Promoting diversified and less competitive weed communities favours the continued provision of  
481 weed ecosystem services, such as support for diversity at higher trophic levels or erosion  
482 mitigation. By measuring the short-term frequency of crop shifts, we were able to show that the  
483 number of crop shifts had a significantly positive effect on the richness and diversity of herbaceous  
484 weed communities. It did not, however, affect their overall abundance. These results show that  
485 yearly crop shifts in this area are not adequate to control weed biomass and their competitiveness  
486 toward the crop, but support plant diversity conservation. Future research should address crop  
487 shifts in longer and diversified crop sequences in these threatened, rapidly changing agro-  
488 ecosystems to further determine their potential for weed control and diversity conservation.

## 489 **Acknowledgements**

490 This study was realised during a research project of Sorbonne University and Institut de  
491 Recherche pour le Développement; and was supported by the ANR HeveAdapt project (grant ANR-  
492 14-CE030012-04) of the French Agence Nationale de la Recherche. Fieldwork was realised with the  
493 cooperation of the Huai Lang Royal Project Center and the Land Development Department of  
494 Thailand. We thank two anonymous reviewers for their thoughtful comments.

## 495 **Data availability**

496 Data and R code used in this study will be made available online upon acceptance.

## 497 **List of Tables**

498 **Table 1. Selected descriptors of plant communities.**

499 **Table 2. Description of crop type in the sampled fields (i.e. from March 2016 onwards) based on the variables**  
500 **annual crop and presence of young trees (rubber or longan). In parenthesis: sample size for dry and rainy season.**

501 **Table 3. Crop sequences between 2013 and 2017. The number of crop shifts is calculated based on the crop**  
502 **types of the three previous growing seasons (see Fig. 1). *Nd*: no available data: the three-years sequence starting**  
503 **with this year was not included.**

504 **Table 4. Effects of crop type and crop shifts on weed richness, diversity and abundance: results from mixed**  
505 **model analyses.**

506 **Table 5. Indicator species associated with fields with zero, one or two crop shifts in the three years preceding**  
507 **sampling. Test statistic is the IndVal.g association index. \*\*\* P < 0.001, \*\* P < 0.01, \* P < 0.05.**

508

## 509 **List of Figures**

510 **Figure 1. Quantification of the number of crop shifts or the number of crop types, over three growing seasons**  
511 **(example crop sequence: maize - maize - maize - rice - fallow). Larger symbols indicate the crop type at the time of**  
512 **sampling, while smaller symbols indicate previous crops. Vertical arrows indicate the time of sampling: for each**  
513 **cropping season, sampling was conducted in the rainy season just after harvest (blue arrow, same calendar year)**  
514 **and in the dry season, 4-5 months after harvest (red arrow, following calendar year).**

515 **Figure 2. Frequency distribution of 22 combinations of crop sequences occurring in farmers' fields over the**  
516 **period 2013-2017. T indicates the presence of young trees, i.e. rubber or longan.**

517 Figure 3. Relative Importance index divides the identified species into three groups: (1) dominant, ubiquitous  
518 species, here *A. conyzoides* (AGECO), *C. sumatrensis* (ERISU) and *M. hirtus* (MTCVI) (top part) (2) intermediate  
519 species (middle part) and (3) rare species (bottom part). Species codes can be found in Table S1.

520 Figure 4. Relationships between species number per field and number of crop shifts. Bars represent the mean +  
521 +/- standard deviation, different letters indicate significant differences ( $P < 0.05$ ) within each group (herbaceous  
522 or shrub/trees).

523

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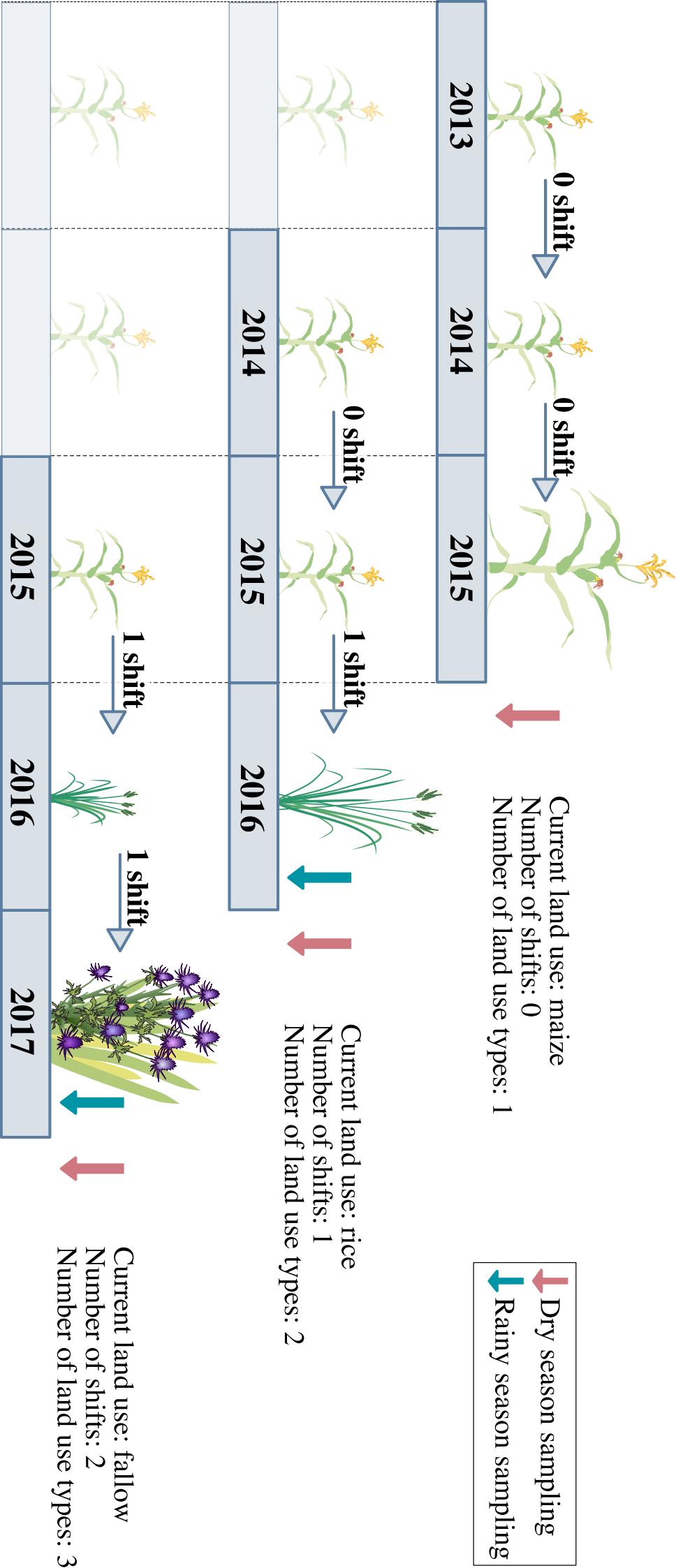
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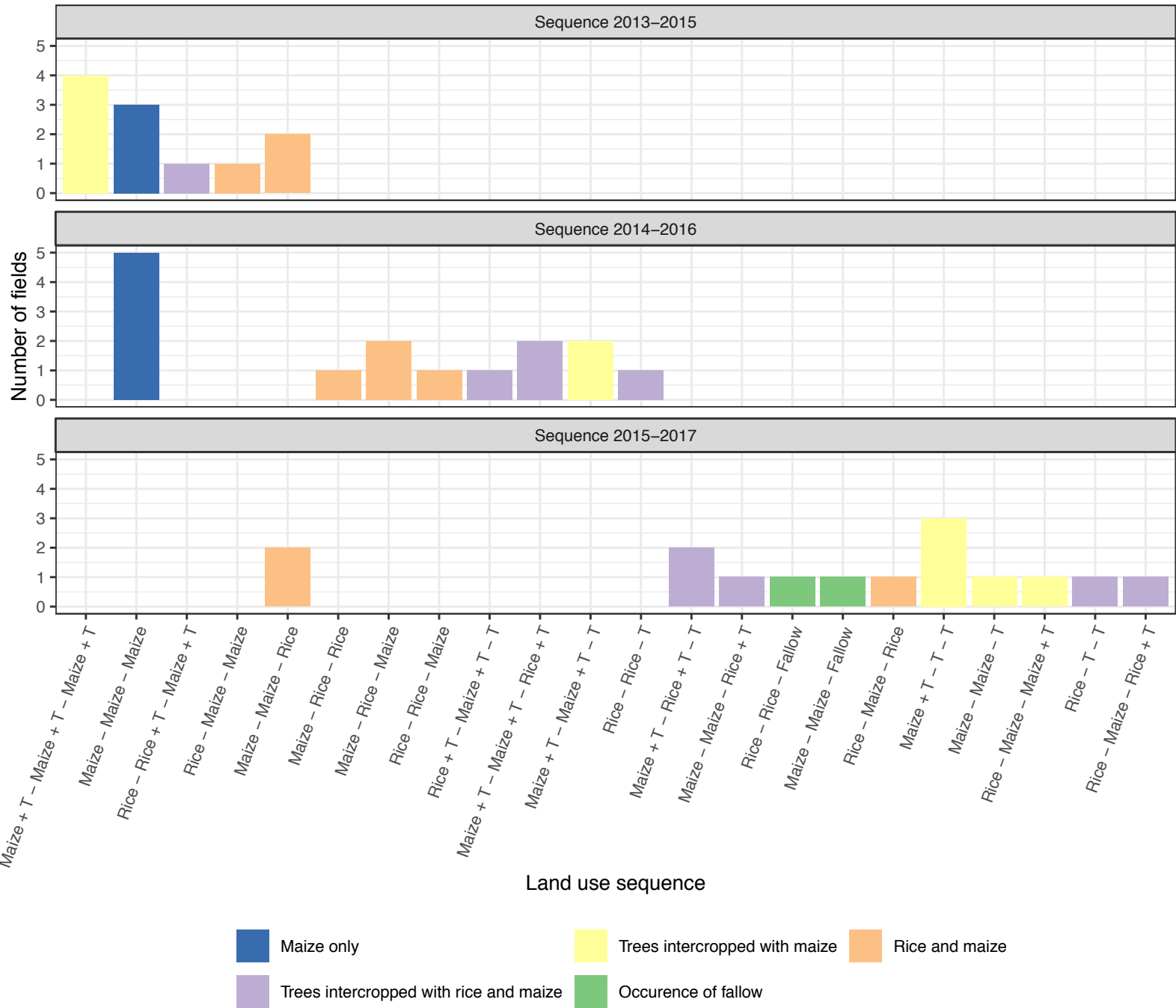
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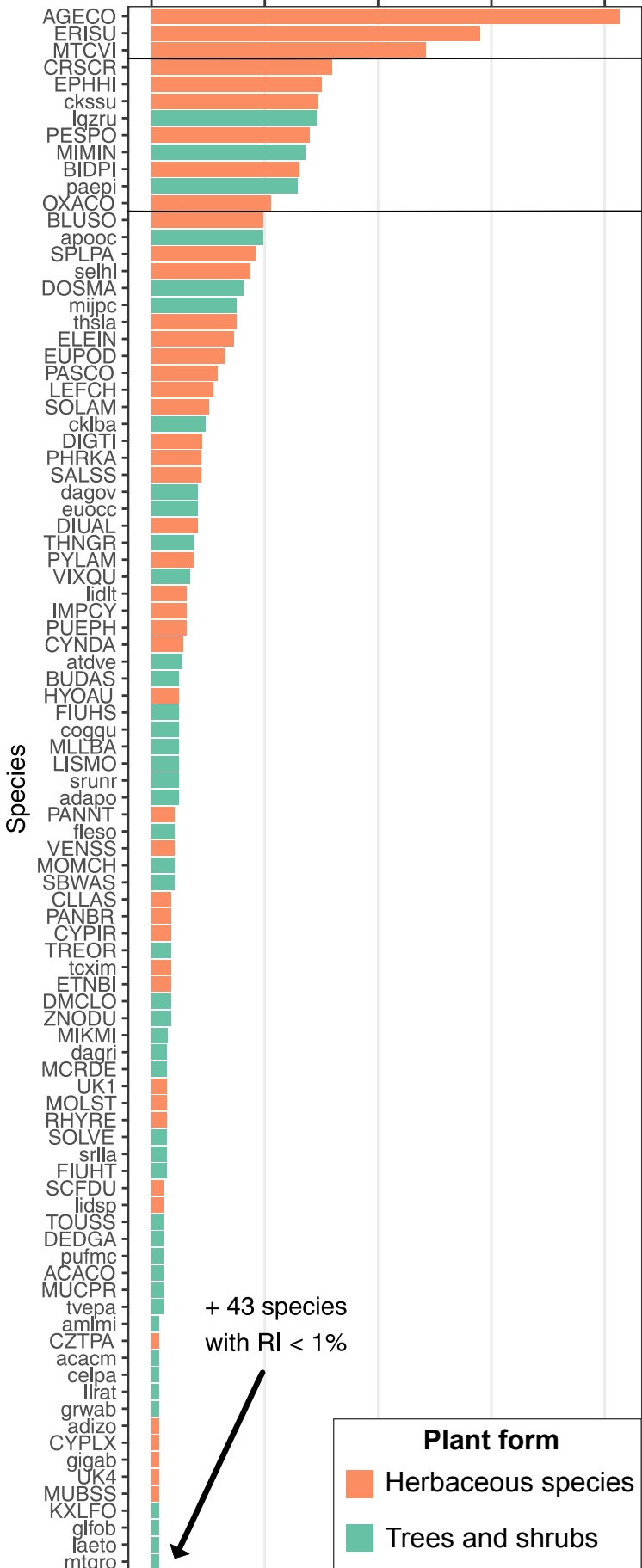




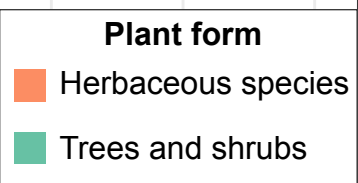


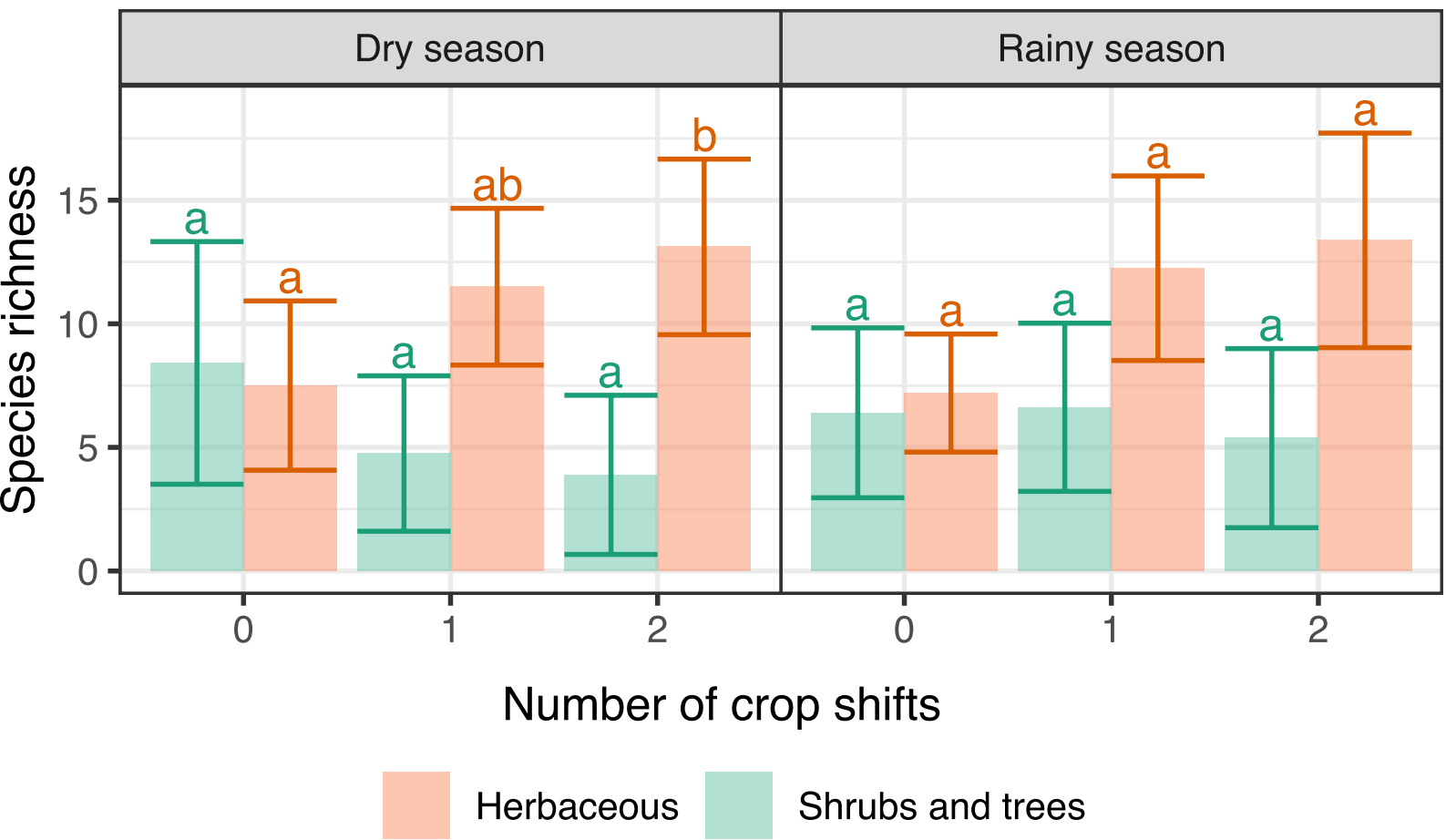
# Relative Importance index

0.0 0.2 0.4 0.6 0.8



+ 43 species  
with RI < 1%





## Tables

Table 1. Selected descriptors of plant communities.

	Name	Calculation	Biological meaning	Details on calculation
	Species number	S (number of species present in the field)	Species richness, simple biodiversity indicator. Provides the size of the local species pool	
Diversity	Shannon index	$H' = -\sum_i p_i \log(p_i)$ with $p_i = \frac{N_i}{N}$ The relative abundance of species i within the field (N <sub>i</sub> : abundance of species i, N : total number of individuals)	Diversity index, which takes into account both the number of species and their diversity. H tends to 0 when one species is ultra-dominant in the community. It tends towards ln(S) when the S species are present in equal abundance in the community.	Calculated separately for herbs and shrubs/trees as well as for all species together
	Berger-Parker index	D = p <sub>i, max</sub> with p <sub>i, max</sub> , max the relative abundance of the most abundant species within the field	Dominance index, measuring the strength of the dominance of the most abundant species. Tends to 1 in monospecific communities and to 1/S when the S species are present in equal abundance in the community.	
Abundance	Plant biomass	Biomass (g) per square meter	Information on ecosystem productivity <sup>2</sup>	Measured for herbaceous, shrub and tree species together
	Plant density	Number of individuals per square meter	Weed reproduction success, competition, soil moisture	

**Table 2. Description of crop type in the sampled fields (i.e. from March 2016 onwards) based on the variables annual crop and presence of young trees (rubber or longan). In parenthesis: sample size for dry and rainy season.**

	<b>Maize</b>	<b>Rice</b>	<b>No annual crop</b>
<b>No young trees</b>	Maize monoculture (dry season: n = 12, rainy season n = 8)	Upland rice monoculture (dry season n = 6, rainy season n = 3)	Fallow (rainy season n = 2, dry season n = 2)
<b>Young trees</b>	Young trees with maize intercrop (dry season n = 6, rainy season n = 1)	Young trees with rice intercrop (dry season n = 8, rainy season n = 8)	Young trees without intercrop (dry season n = 11, rainy season n = 11)

**Table 3. Crop sequences between 2013 and 2017. The number of crop shifts is calculated based on the crop types of the three previous growing seasons (see Fig. 1). *Nd*: no available data: the three-years sequence starting with this year was not included.**

Field	Crop sequence					Number of crop shifts <sup>1</sup>		
	2013	2014	2015	2016	2017	2013-2015	2014-2016	2015-2017
1	<i>nd</i>	Maize	Maize	Maize	Longan tree + Rice		0	1
2	Maize	Maize	Maize	Maize	Rubber tree + Fallow	0	0	1
3	Maize	Maize	Maize	Maize	Rice	0	0	1
4	Maize	Maize	Maize	Maize	Rice	0	0	1
5	Rice	Maize	Maize	Maize	Fallow	1	0	1
6	<i>nd</i>	Maize	Rice	Rice	Fallow		1	1
7	Maize	Maize	Rice	Maize	Longan tree + Maize	1	2	2
8	<i>nd</i>	Rice	Rice <sup>2</sup>	Maize	Longan tree + Rice		1	2
9	Maize	Maize	Rice	Maize	Rice	1	2	2
10	<i>nd</i>	Rice	Rice	Longan tree + Fallow	Longan tree + Fallow		1	1
11	Rubber tree + Maize	Rubber tree + Maize	Rubber tree + Maize	Rubber tree + Rice	Rubber tree + Fallow	0	1	2
12	Rubber tree + Maize	Rubber tree + Maize	Rubber tree + Maize	Rubber tree + Rice	Rubber tree + Fallow	0	1	2
13	Rubber tree + Maize	Rubber tree + Maize	Rubber tree + Maize	Rubber tree + Fallow	Rubber tree + Fallow	0	1	1
14	Rubber tree + Maize	Rubber tree + Maize	Rubber tree + Maize	Rubber tree + Fallow	Rubber tree + Fallow	0	1	1
15	Rice	Rubber tree + Rice	Rubber tree + Maize	Rubber tree + Fallow	Rubber tree + Fallow	2	2	1

<sup>1</sup> The crop shift counting of the periods 2013-2015; 2014-2016; and 2015-2017 correspond respectively to the weed sampling in March 2016; November 2016 and March 2017; November 2017 and March 2018.

<sup>2</sup> Sampled in the dry season only.

**Table 4. Effects of crop type and crop shifts on weed richness, diversity and abundance: results from mixed model analyses.**

**a. Pseudo-partial R<sup>2</sup> of each explanatory variable and global R<sup>2</sup> (Kenward Roger method) in percent. \*: P < 0.05. \*\*: P < 0.01. \*\*\*: P < 0.001. A dot denotes an insignificant trend (P < 0.1).**

	Number of crop shifts	Season	Shifts x season	Annual crop	Presence of trees	Global R <sup>2</sup>
Species number (all species)	4 n.s	1 n.s	7 n.s	0 n.s	0 n.s	15
Species number (herbaceous species)	13 **	1 n.s	0 n.s	6 n.s	2 n.s	37
Species number (tree and shrub species)	2 n.s	0 n.s	12 *	3 n.s	4 n.s	21
Dominance (all species)	10 *	21 ***	2 n.s	8 .	0 n.s	29
Dominance (herbaceous species)	12 **	14 **	3 n.s	9 *	0 n.s	29
Dominance (tree shrub species)	0 n.s	1 n.s	0 n.s	3 n.s	1 n.s	4
Shannon index (all species)	7 .	17 **	4 n.s	1 n.s	0 n.s	23
Shannon (herbaceous species)	10 *	9 *	5 n.s	1 n.s	2 n.s	25
Shannon (tree and shrub species)	0 n.s	0 n.s	0 n.s	2 n.s	1 n.s	3
Biomass (square-root transformed, all species)	5 n.s	6 n.s	4 n.s	11 *	17 **	23
Density (log, all species)	1 n.s	13 *	4 n.s	1 n.s	2 n.s	17

**b. Estimates for each number of crop shifts, presented as average (confidence interval). Different letters indicate differences significant at a 5% threshold. Responses with significant responses are represented in bold.**

	Number of crop shifts	Estimate (dry season)	Estimate (rainy season)
Richness (all species)	0	15.7 (11.4 - 20) <sup>a</sup>	13.4 (7.9 - 18.9) <sup>a</sup>
	1	16.2 (13.5 - 18.9) <sup>a</sup>	19.1 (16.2 - 22.1) <sup>a</sup>
	2	17.1 (13.4 - 20.8) <sup>a</sup>	19.5 (15.6 - 23.4) <sup>a</sup>
<b>Richness (herbaceous species)</b>	0	<b>8.3 (5.3 - 11.2) <sup>a</sup></b>	<b>8.7 (5 - 12.4) <sup>a</sup></b>
	1	<b>11.4 (9.6 - 13.3) <sup>ab</sup></b>	<b>12.3 (10.3 - 14.4) <sup>ab</sup></b>
	2	<b>13 (10.4 - 15.6) <sup>b</sup></b>	<b>13.7 (11 - 16.4) <sup>b</sup></b>
Richness (tree and shrub species)	0	7.4 (4.3 - 10.4) <sup>a</sup>	4.7 (0.9 - 8.5) <sup>a</sup>
	1	4.7 (2.8 - 6.6) <sup>a</sup>	6.8 (4.7 - 8.9) <sup>a</sup>
	2	4.2 (1.6 - 6.8) <sup>a</sup>	5.8 (3 - 8.5) <sup>a</sup>
<b>Dominance (all species)</b>	0	<b>0.7 (0.6 - 0.9) <sup>a</sup></b>	0.9 (0.7 - 1.1) <sup>a</sup>
	1	<b>0.6 (0.5 - 0.7) <sup>ab</sup></b>	0.7 (0.6 - 0.8) <sup>a</sup>
	2	<b>0.5 (0.4 - 0.6) <sup>b</sup></b>	0.7 (0.5 - 0.8) <sup>a</sup>
<b>Dominance (herbaceous species)</b>	0	<b>0.8 (0.7 - 1) <sup>a</sup></b>	0.9 (0.7 - 1.1) <sup>a</sup>
	1	<b>0.6 (0.5 - 0.7) <sup>a</sup></b>	0.7 (0.6 - 0.8) <sup>a</sup>
	2	<b>0.5 (0.4 - 0.7) <sup>b</sup></b>	0.7 (0.6 - 0.8) <sup>a</sup>
Dominance (tree and shrub species)	0	0.7 (0.5 - 0.9) <sup>a</sup>	0.7 (0.4 - 1) <sup>a</sup>
	1	0.7 (0.6 - 0.8) <sup>a</sup>	0.7 (0.6 - 0.9) <sup>a</sup>



	2	0.7 (0.5 - 0.9) <sup>a</sup>	0.8 (0.6 - 0.9) <sup>a</sup>
<b>Shannon index</b>	0	<b>1 (0.6 - 1.3) <sup>a</sup></b>	0.7 (0.3 - 1.2) <sup>a</sup>
<b>(all species)</b>	1	<b>1.2 (1 - 1.4) <sup>ab</sup></b>	1 (0.7 - 1.2) <sup>a</sup>
	2	<b>1.5 (1.2 - 1.8) <sup>b</sup></b>	1 (0.6 - 1.3) <sup>a</sup>
<b>Shannon</b>	0	<b>0.7 (0.3 - 1) <sup>a</sup></b>	0.6 (0.2 - 1.1) <sup>a</sup>
<b>(herbaceous species)</b>	1	<b>1 (0.8 - 1.2) <sup>ab</sup></b>	0.8 (0.6 - 1.1) <sup>a</sup>
	2	<b>1.3 (1 - 1.6) <sup>b</sup></b>	0.9 (0.6 - 1.2) <sup>a</sup>
Shannon	0	0.7 (0.3 - 1.2) <sup>a</sup>	0.7 (0.2 - 1.3) <sup>a</sup>
(tree and shrub species)	1	0.7 (0.4 - 1) <sup>a</sup>	0.6 (0.3 - 0.9) <sup>a</sup>
	2	0.6 (0.3 - 1) <sup>a</sup>	0.6 (0.2 - 1) <sup>a</sup>
Biomass	0	7.5 (3.6 - 11.4) <sup>a</sup>	2.3 (-2.9 - 7.4) <sup>a</sup>
(square-root	1	8.8 (6.4 - 11.1) <sup>a</sup>	7.9 (5.3 - 10.6) <sup>a</sup>
transformed, all species)	2	7.6 (4.3 - 10.9) <sup>a</sup>	6.8 (3.3 - 10.2) <sup>a</sup>
Density	0	5.4 (4.5 - 6.2) <sup>a</sup>	6.2 (5 - 7.3) <sup>a</sup>
(log-transformed, all	1	5.6 (5 - 6.1) <sup>a</sup>	5.8 (5.2 - 6.4) <sup>a</sup>
species)	2	5.4 (4.6 - 6.2) <sup>a</sup>	6.4 (5.6 - 7.2) <sup>a</sup>

**Table 5. Indicator species associated with fields with zero, one or two crop shifts in the three years preceding sampling. Test statistic is the IndVal.g association index. \*\*\* P < 0.001, \*\* P < 0.01, \* P < 0.05.**

<b>Growth form</b>	<b>Species</b>	<b>Test statistic</b>	<b>Significance</b>
<b>Fields with zero shift</b>			
Tree	<i>Antidesma velutinsum</i>	0.534	*
Shrub	<i>Streblus asper</i>	0.485	*
Liana	<i>Tournefortia sp.</i>	0.420	*
<b>Fields with zero to one shift</b>			
Tree	<i>Diospyros malabarica</i>	0.629	*
Large liana	<i>Millettia pachycarpa</i>	0.599	*
<b>Fields with one to two shifts</b>			
Ground fern	<i>Thelepterys subelatus</i>	0.830	***
Annual herb	<i>Bidens pilosa</i>	0.749	*
Perennial C <sub>3</sub> grass	<i>Thysanolaena latifolia</i>	0.625	*
<b>Fields with two shifts</b>			
Annual C <sub>4</sub> grass	<i>Digitaria radicata</i>	0.547	**
Tree	<i>Vitex quinata</i>	0.510	*
Perennial herb	<i>Centella asiatica</i>	0.479	**
Perennial vine	<i>Thunbergia grandiflora</i>	0.475	*

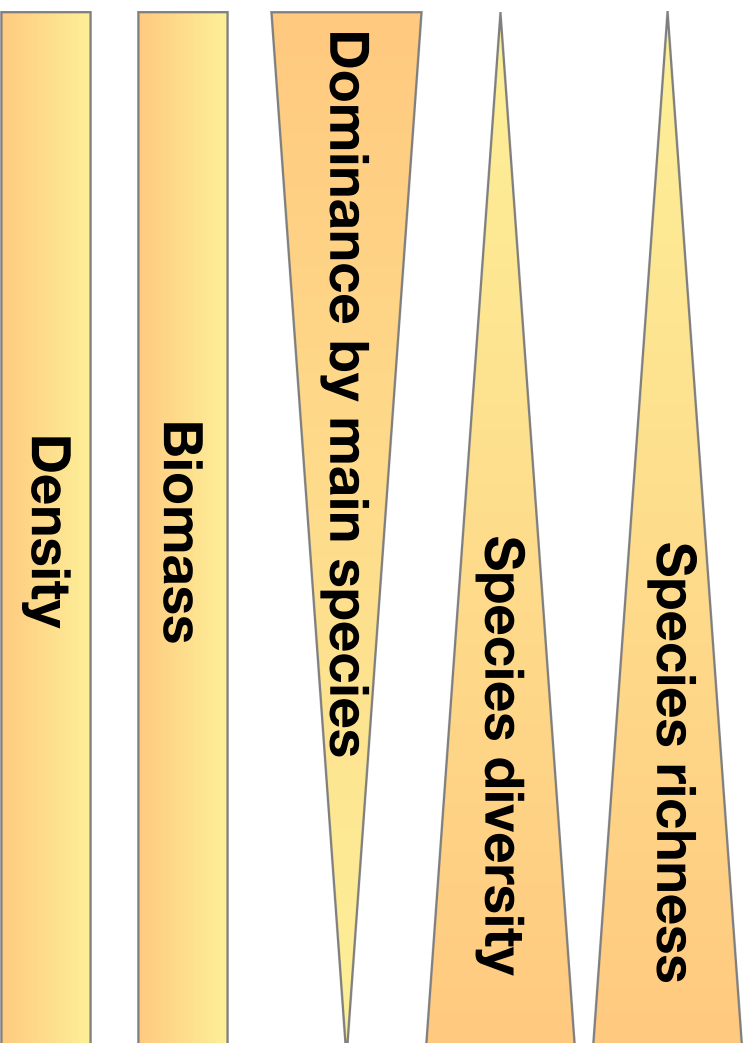


*Crop sequences*

**0 shift**



**2 shifts**



*Weed communities*