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1 **Anecic earthworms generate more topsoil than they contribute to erosion – evidence at**
2 **catchment scale in northern Vietnam**

3

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27 **Abstract**

28 Soil is considered as a non-renewable resource, which may be lost in sloping land more
29 rapidly than it its formed thus leading to loss of fertility and ecosystem deterioration. We
30 hypothesized that earthworms could counteract this process due to their cast forming activity.
31 To test this hypothesis, we quantified the production of casts in small plots of 0.25 m²
32 established in three vegetation units (woodland, shrubland and meadow) in a catchment of 50
33 ha for 2.5 years in relation to their (micro-) pedoclimatic conditions. We also assessed their
34 impact on water runoff and soil detachment. Moreover, we quantified the mass of casts
35 deposited in the entire catchment on a regular grid of 50 m and we measured soil erosion at
36 the outlet of the catchment.

37

38 Our results showed a high and variable production of casts (from 16 to 219 t ha⁻¹ year⁻¹)
39 depending on vegetation, season and year. The mass of casts found in the entire catchment
40 represented on average 7.5 t ha⁻¹ with an annual production rate of 36 t ha⁻¹. Since the annual
41 erosion rate measured for the entire catchment (3 t ha⁻¹ year⁻¹) was much lower than the cast
42 production rate, our results indicated that most of the soil bioturbated by earthworms
43 remained in the catchment. Indeed, water runoff and soil detachment measured in small plots
44 showed that casts were not transported in the water runoff but degraded by raindrop impacts
45 with the material remaining at the place of deposition. This process led to the generating of a
46 new soil horizon at the culmination point of the catchment of up to 6.5 cm after 2.5 years. We
47 conclude that the surface activity of anecic earthworms could influence soil generation at
48 scale and reverse the effects of soil erosion.

49

50 **Keywords:** tropical soil, bioturbation, earthworm cast

51 **1. Introduction**

52 Earthworms ingest and transform huge amounts of organic and inorganic material,
53 corresponding to up to 30 times their own weight per day (Lavelle, 1975). As a result they
54 deposit organic matter rich aggregates at the soil surface (casts), which impact numerous soil
55 functions, such as those associated to the dynamic of carbon and nutrients (Van Groenigen et
56 al., 2019). High casting activity and stability of these structures are also considered to (1)
57 shape the organization of soil structure (Lavelle et al., 2020), (2) explain the granular
58 organization of A horizons in many ecosystems (Jongmans et al., 2003), and (3) the burial of
59 archaeological items (Darwin, 1881; Stein, 1983). Despite their significant influence on main
60 ecological functions in soil, a major obstacle to the quantification and modeling of the
61 influence of earthworms on soil functioning lies in the fact that the amount and dynamics of
62 casts produced at landscape scale remain poorly documented.

63 Surface earthworm casting activity is highly variable and reaches its record in the
64 tropics with $250 \text{ t ha}^{-1} \text{ year}^{-1}$ measured in Nigeria (Madge, 1969). Once deposited on the soil
65 surface, casts are degraded by the rain and/or by the trampling of large animals depending on
66 environmental and ecological factors. For instance, the production and degradation of casts is
67 expected to be higher in tropical than in temperate environments, because of higher
68 temperature and higher precipitations and greater biological activity. Vegetation may protect
69 casts from destruction though raindrop impacts and extend their lifespan (Decaëns, 2000).
70 However, based on our visual assessment in the field, we hypothesized that the casts'
71 resistance to erosion also depends on soil properties such as their carbon and clay content or
72 on the cast type (granular < past-like < globular) formed in different situations. If not
73 degraded on site, casts can also contribute to the sediment load following water erosion,
74 especially in tropical sloping land (Blanchart et al., 2004; Jouquet et al., 2010). Generally, the
75 impact of erosion on the fate of earthworm casts was estimated from indicators, as for

76 example soil aggregate stability to water or measured directly in the field at small scale on
77 erosion plots under natural or simulated rainfalls (Hazelhoff et al., 1981; Jouquet et al.,
78 2008b, 2012, 2013; Le Bayon et al., 2002; Le Bayon and Binet, 1999, 2001; Podwojewski et
79 al., 2008; Sharpley and Syers, 1976). These approaches are not necessarily representative of
80 the processes taking place at the landscape scale.

81 Dry and water-stable casts are usually considered to be resistant to raindrop impact.
82 They increase soil roughness and water infiltration (i.e. reduce water runoff), reduce soil
83 detachment and protect soil from crusting (Jouquet et al., 2012). In contrast, freshly emitted
84 casts are unstable, prone to dislocation and can increase seal formation and soil loss by
85 erosion (Le Bayon et al., 2002; Le Bayon and Binet, 2001). Therefore, the casting activity
86 could contribute to soil accrual or its erosion. The occurrence of both phenomena may vary
87 in different landscape positions due to microclimatic conditions.

88 This study investigated the balance of both processes to answer the question if
89 earthworms contribute more to soil accrual or its erosion. We addressed this issue by
90 quantifying the impact of earthworm casting activity at the landscape scale in a tropical
91 sloping catchment (50 ha). To this end, we established small plots (0.25 m²) under three
92 vegetation units and quantified (1) casts produced by the anecic earthworm *Amyntas adexilis*
93 and (2) their impact on water runoff and soil detachment during 2.5 years. Additionally, we
94 assessed cast production in the entire catchment by grid sampling and measured soil
95 transported out of the catchment. We hypothesized that (1) earthworm casting activity is
96 influenced by climatic variables and shows highest activity during the rainy season, and (2)
97 that cast production might counteract soil erosion.

98

99 **2. Methods**

100 **2.1. Study site**

101 This study was carried out from 2016 to 2018 in a tropical catchment located in Dong Cao
102 village in the North of Vietnam (20° 57'N, 105° 29'E). The site belongs to the M-Tropics
103 long-term observatory. The Dong Cao catchment with an area of 46 ha is located on sloping
104 land with an average slope of 40%, locally exceeding 100%. Annual rainfall varied from 1770
105 mm in 2017 to 2224 mm in 2018. The annual air temperature was 23°C in 2017 and 2018.
106 The dry season lasting from November to April and was characterized by the lowest
107 precipitation (222 mm) and air temperature (19 °C). The wet season lasting from May to
108 October and was characterized by the greatest precipitation (1688 mm in 2017 and 1922 mm
109 in 2018) and air temperature (27 °C). The dominant soil type in the catchment is Acrisol
110 (Podwojewski et al., 2008), derived from the weathering of volcano-sedimentary schists of
111 Mesozoic age. Soils are over 1 m deep but with marked variation in thickness. Their clay
112 content is higher than 50% and they are very porous with a bulk density of 1 g cm⁻³. They
113 have a homogenous brown color (10 YR 4/4 to 7.5 YR 4/6), and a weak differentiation. The
114 clay fraction is almost exclusively composed of kaolinite with a low CEC. The catchment is
115 covered by woodlands, secondary forests, meadows and shrublands. Surface earthworm
116 activity in the catchment is high with the earthworm *Amyntas adexilis*, formerly identified as
117 *Amyntas khami* (Jouquet et al., 2008a) as the only species. It belongs to the ecological
118 category of anecic earthworms, which show vertical borrowing activity with deposition of
119 earthworm casts at the soil surface. The casts of *Amyntas adexilis* reach 20 cm length and are
120 produced through an accumulation of fecal pellets deposited the one on the other (Fig. 1).
121 They are always enriched in organic C and can be more water stable than the surrounding soil
122 depending on their degradation stage (Bottinelli et al., 2021; Le Mer et al., 2021). In addition,
123 *A. adexilis* digs vertical burrows that are connected to the surface and can act as preferential
124 pathways for water flow (Le Mer et al., 2021).

125

126 **2.2. Earthworm cast production and soil detachment at the plot scale**

127 Eight plots of 0.25 m² were set up from July 2016 to December 2018 in each of the three
128 representative vegetation units (woodland, shrubland and meadow) to measure the casting
129 activity of *A. adexilis* and its impact on runoff and soil detachment. The plot location was
130 chosen randomly in each vegetation unit to account for the field variability of earthworm
131 casting activity. The mean slope was 24, 17 and 13 degrees in woodland, shrubland and
132 meadow, respectively. In each vegetation unit, four plots were kept untouched, while four
133 other plots were used to quantify the weekly production of casts. All earthworm casts were
134 removed from plots before the beginning of the experiment.

135 Rigid metal frames (50 cm height) were inserted to a depth of 5 cm and used to delimit plots.
136 A 30 L bucket was put at the outlet of each plot to collect runoff water and sediment. Soil
137 height was measured twice (July 2016 and December 2018) on 110 regular points using a
138 laser distance meter. Soil detachment and water runoff were collected five times at the end of
139 the rainy season in 2018 (18 of August, 1, 22, 29 of September and 27 of October). The total
140 volume of runoff was calculated from the measurement of water height in the collecting
141 bucket. The runoff coefficient corresponded to the ratio of the runoff divided by rainfall. The
142 concentration of soil particles was measured from a 500 mL aliquot, which was filtered and
143 weighted after air-drying. We calculated soil detachment as the product of the sediment
144 concentration in the collected samples and the runoff volume. Cast production was measured
145 through the sampling and weighing of casts after oven drying at 105°C during 24 h. At the
146 end of the experiment (December 2018), all remaining casts were collected from the
147 untouched plots and weighed in the field. Subsamples were taken to the laboratory to
148 determine their moisture after drying them in an oven at 105°C during 24 h gravimetrically.
149 The sum of cast mass collected every week minus the mass of casts collected after 2.5 years

150 in the untouched plots was used to assess the mass of casts transformed into soil or washed
151 away out of the plots by water runoff.

152

153 **2.3. Earthworm cast production and soil erosion at the catchment scale**

154 The sampling took place in February 2017, during the dry season because of the difficulty of
155 walking in the catchment during the rainy season. 195 points were sampled on a regular grid
156 (50 x 50 m) covering the entire catchment. At each point, on three replicates of 1 m², casts
157 were classified into three groups (i) active (standing and wet); (ii) non-active (stand and dry)
158 and (iii) degraded (dry and broken). The number of active and non-active casts was quantified
159 and the weight of the three categories was determined in the field and corrected for moisture,
160 which was determined on subsamples dried in the oven at 105°C during 24h.

161 Soil erosion at the catchment scale was measured at the outlet of the catchment using a V-
162 notch weir. Suspended sediments were collected using an automatic water sampler. The
163 automatic sampler was triggered by the water level recorder to collect water after every 2-cm
164 water level change during flood rising and every 5-cm water level change during flood
165 recession. The concentration of suspended particulate matter in each sample was measured
166 after filtration and evaporation at 105 °C for 48 h. Bed particulate matter was determined
167 from the sediments that were retained in the stilling basins of the weir. Monthly, or if the
168 basin was full, the volume of deposited sediments was measured considering a density of 1 g
169 cm⁻³ for soft sediments and of 2.65 g cm⁻³ for stones. The annual erosion rate represented
170 the cumulative suspended and bedload sediments divided by the catchment area.

171 An automatic weather station measuring on a one-minute basis the temperature and
172 precipitation was located at the bottom of the catchment. Soil temperature sensors were buried
173 at 10 cm depth and watermark sensors were buried at 5, 10, 30, 50, 100, 150 cm depth to

174 continuously monitor soil temperature and soil water tension (0- 250 cm) in the three
175 vegetation units.

176

177 **2.6. Statistical analyses**

178 One-way ANOVA and repeated measures ANOVA were performed to test the effect of the
179 vegetation unit and the sampling time on the production of casts in the 0.25 m² plots,
180 respectively. T-test was used to test the effect of presence or absence of earthworm casts on
181 water runoff and soil detachment in 0.25 m² plots for each vegetation unit. Prior to running
182 ANOVA and T-test, data were tested for homogeneity of variances and normality.
183 Differences among treatments were declared significant at the 0.05 probability level.
184 Between-class analysis (BCA) and Monte Carlo permutation tests (1000 permutations) was
185 carried out to discriminate the three vegetation units in 2017 and 2018 in function of soil and
186 air temperature and water tension. BCA measures the amount of variance restricted to the
187 grouping factor as a percentage of the total inertia (Dray et al., 2011). Random forest
188 regression was used to identify climatic variables influencing cast production in each
189 vegetation unit. Random forest is a nonparametric method, which consists of a large number
190 of individual tree models trained from bootstrap samples of the data (Breiman, 2001). The
191 results of all individual trees are aggregated to make a single prediction. The variables tested
192 in were total precipitations, precipitations > 20 mm h⁻¹, air temperature, soil temperature and
193 soil water tension from 10 to 150 cm depth. The dataset for each vegetation unit represented
194 115 measurements of cast production and was randomly split into calibration dataset (80%)
195 and validation dataset (20%). The optimization of parameters for the final models was based
196 on minimizing the root mean square error (RMSE) between the measured and the estimated
197 value of the production of casts for the calibration dataset based on 10-fold repeated cross-
198 validation with five repetitions. The number of variables for each tree (mtry) and the number

199 of trees in the forest (ntree) are two user-defined parameters which need to be optimized. The
200 number of trees (ntree) was 1000 in this study. Mtry was identified as those returning the
201 lowest RMSE by iterating mtry values from 1 to 11 representing the number of predictors.
202 The relative importance of variables was estimated from the mean decrease in predictive
203 accuracy. The model performances for prediction of the production of casts on the test dataset
204 were evaluated using coefficient of determination (R^2), root mean square error of prediction
205 (RMSE) and residual predictive deviation (RPD). The RPD denotes the ratio of the standard
206 deviation of the measured cast production to the RMSE calculated between the measured and
207 predicted cast production.

208 The relationship between the number of casts collected in the three vegetation units
209 after one week of production in February 2017 and the cumulative mass of casts produced for
210 2017 for each plot was calculated. The relationship was used to predict the mass of casts
211 produced in 2017 at every grid sampling points using the number of active casts collected
212 during the sampling of earthworm casts at catchment scale in February 2017. All statistical
213 calculations and plots were carried out using R software using ‘caret’, ‘car’, ‘agricolae’ and
214 ‘ggplot2’ packages.

215

216 **3. Results**

217 **3.1. Earthworm cast production at the plot scale and consequence on soil detachment**

218 The production of casts at the plot scale varied from 16 to 220 t ha⁻¹ year⁻¹ and decreased in
219 the order meadow>woodland>shrubland (p < 0.01) (Fig. 2). The production of casts was
220 higher in 2017 than 2018 in woodland and meadow (p < 0.01 for in both cases), whereas the
221 opposite was found in shrubland (p < 0.05). In shrubland and meadow, the production
222 followed a periodicity of 6 months with lowest values occurring in December and July. In
223 woodland, cast production followed a periodicity of 12 months with lowest values in

224 December. We used random forest models to investigate the climatic variables influencing the
225 cast production at plot scale. These models did not perform well at predicting the mass of
226 casts with ratio of prediction deviation (RPD) of 1.2, 1.1 and 1.2 for the woodland, shrubland
227 and meadow, respectively (Fig. 3a). For the shrubland and meadow, the most important
228 variables (Fig. 3b) explaining the production of casts were related to soil water tension (at 150
229 and 5 cm depth in shrubland and meadow, respectively). Conversely in the woodland, the
230 most important variable was soil temperature.

231 The production of casts led to the formation of a new horizon (Fig. 4a) reaching up to
232 6.5 cm after 2.5 years (Fig. 4b). The degradation of casts measured for 2.5 years represented
233 between 2 to 34 kg m⁻² (Fig. 4c).

234 For the five rain events combined (152, 207, 80, 69 and 148 mm of precipitations),
235 runoff coefficient (Fig. 5a) and soil detachment (Fig. 5b) were greatest in the absence of casts.
236 However, results were only statistically significant for the soil detachment in meadow.

237

238 **3.2. Earthworm cast production and soil erosion at the catchment scale**

239 Cast production in the entire catchment was evaluated in February 2017. The mass of casts
240 found in the catchment varied from 0 to 6.5 kg m⁻² and represented on average 7.5 t ha⁻¹ (Fig.
241 6). 80% of the casts showed a degraded aspect. The number of active and non-active casts
242 varied between 0-13 and 0-14 per m², respectively. The number of casts collected in 0.25 m²
243 plots after one week of production in February 2017 varied between 0 to 20 per m⁻² and was
244 positively related ($R^2 = 0.90$) to the total mass of casts collected during the year (Fig. 7).
245 Using this relationship for assessing the annual mass of casts produced in the entire catchment
246 with the number of active casts, we predicted that the cast production amounted on average to
247 36 t ha⁻¹ of casts in 2017 (from 0.2 to 1.7 cm of soil using a bulk density of 1 g cm⁻³). This is
248 5 times higher than the cast mass observed on average at catchment scale (see above) and 12

249 times higher than the annual erosion rate measured at the outlet of the catchment, which
250 represented only 3 t ha⁻¹.

251

252 **4. Discussion**

253 **4.1. Earthworm cast production varies in space and time**

254 The quantity of surface casts produced in the three vegetation units during the years 2017 and
255 2018 varied from 16 to 220 t ha⁻¹ at plot scale (i.e., between 0.2 to 2.2 cm of soil considering
256 the soil bulk density of 1 g cm⁻³), which is of the same order of magnitude as was found in
257 other tropical regions (Hauser et al., 2012; Madge, 1969). The most important factor
258 explaining this variability is the vegetation. Differences are most likely linked to the
259 abundance of earthworms and not their activity since soil properties (data not shown) and soil
260 climate were relatively similar between vegetation units. Indeed, assuming that the number of
261 fresh casts quantified every week is an estimation of the number of individuals per plot
262 (Jiménez et al., 1998), the density of *A. adexilis* may be different between the three vegetation
263 units (Fig. 7). Temperature and rainfall intensity changes throughout the year had strong
264 impacts on the production of casts. In the three vegetation units, decreasing cast production
265 was found in December, when the air temperature and precipitation were the lowest. This is in
266 agreement with other studies, which found relationships between cast production and soil
267 temperature (Whalen et al., 2004) and moisture (Zaller and Arnone III, 1997).

268

269 In the shrubland and meadow, a decrease of activity was also recorded in July, when the air
270 temperature and rainfall were highest. Since the pedoclimatic conditions were similar for the
271 three vegetation units during the wet season, discrepancies might be linked to microclimatic
272 variations affecting the degradation casts at the three sites. While earthworm casts after drying
273 exhibit high aggregate stability as compared to physical soil aggregates (Jouquet et a., 2008),

274 recently formed casts are relatively unstable (Le Mer et al., 2021) and may be degraded by
275 rainfall impact. In fact, casts were fully exposed to high intensity precipitations in shrubland
276 and meadow, whereas in woodland they were partly protected by the tree canopy. From 2017
277 to 2018, we measured lower cast production in woodland (by 50%) and meadow (by 20%).
278 This may be partly explained by cast disintegration by rainfall impact, since the precipitations
279 were higher by 454 mm in 2018 as compared to 2017. Moreover, contrasting impacts of
280 precipitation events on earthworm abundance and activity under the three vegetation units
281 cannot be excluded.

282

283 Surprisingly, the production of casts in shrubland increased by 100% from 2017 to 2018. This
284 increase may result from the large spatial variability of earthworm activity in shrubland and
285 the small size plots for the quantification of casts. In 2017, only half of the plots were
286 colonised by earthworms, whereas in 2018 casts were found on the four plots. In this study
287 we consequently showed that rainfall may have positive impacts and negative impacts on the
288 production of casts depending on the vegetation. This combined effect might explain the
289 relatively low accuracy of the random forest models to predict the production of casts. We
290 suggest that the accuracy of the models may be improved in two ways: by measuring other
291 variables (i) linked to the activity of earthworms, such as plants biomass and litter production,
292 which in turn affect earthworm food supply and (ii) linked to the occurrence of splash erosion
293 (e.g. the intensity of the precipitation and the size of the drops in each vegetation units). In
294 other studies, mesh protection was used to measure only the production of casts by protecting
295 the casts from rain splash (Hauser and Asawalam, 1998). However, this method also
296 influenced the measured variable (Le Bayon and Binet, 1999) by maintaining high soil
297 moisture and most likely changing the amount of food supply for earthworms.

298

299 **4.2. Earthworms generate more topsoil than they contribute to erosion**

300 At the plot scale, the accumulation of casts for 2.5 years formed a vermic horizon of up to 6.5
301 cm height. This value is much higher than results found in England (Butt et al., 2016; Darwin,
302 1881) showing that the rate of flint burial by the surface casting activity of anecic earthworms
303 varied from 0.21 to 0.96 cm year⁻¹. We assessed that the degradation of casts accounted
304 between 2 and 34 kg m⁻² for the 2.5 years of experiment. Comparing these figures with the
305 amount of cast transported as sediment in water runoff (i.e., maximum of 100 g m⁻² for four
306 months during the rainy season in 2018), it is clear that casts once degraded were not
307 transported by runoff out of the plots. It is therefore surprising that despite the huge
308 production of casts and obvious cast degradation, the amount of sediments in the runoff water
309 was similar in plots with and without casts. Thus, we hypothesize that high density of water
310 stable casts acted as physical barriers toward the runoff, which promoted the redistribution of
311 eroded casts on a very short distance through successive deposition/suspension processes. Our
312 results were also in agreement with studies carried out at the same study site in 1m² plots
313 showing a negative relationship between the density of earthworm casts and soil detachment
314 (Jouquet et al., 2012; Podwojewski et al., 2008).

315 At the catchment scale, the mass of casts reached at several locations large amounts of
316 up to 6.5 kg m⁻². This led to the formation of a vermic horizon as it was observed in the 0.25
317 m² plots under all three vegetation units. However, the high percentage of broken casts
318 covering the soil indicated that casts were rapidly degraded. Several factors might be involved
319 such as the raindrop impacts, the trampling of buffalo and the activity of soil organisms. We
320 assessed by a linear relationship, that for 2017, the amount of casts produced in the catchment
321 was 5 times higher than what we measured during the survey in February in 2017. This
322 indicates that up to 79% of all cast produced may be degraded within one year. If all the
323 degraded materials were washed away contributing to material leaving the catchment, the

324 annual erosion rate would have been much higher than 3 t ha⁻¹. Therefore, we assume that the
325 material composing earthworm casts remained within the catchment after their degradation.

326 Our results provide evidence that earthworms are strongly involved in redistribution of
327 soil material in this tropical catchment and do not promote soil erosion. In tropical catchments
328 with high bioturbation, earthworms' influence on soil fertility and climate change mitigation
329 may thus be considerable through the formation of organic matter rich horizons. The depth of
330 vermic horizons occurring throughout the catchment may be depending on the landscape
331 position. While the earthworm casting activity may be influenced to some extent by weather
332 conditions, vegetation cover could control the accumulation of the vermic horizon because it
333 may influence casting activity by impacting earthworm abundance and their activity.
334 Moreover, vegetation also influenced the disintegration of casts after their deposition.
335 Therefore, the occurrence of vegetation types and soil accrual may be related with higher soil
336 formation rates occurring under meadow as compared to shrubland and woodland. Vegetation
337 type is thus important to consider at the landscape scale in addition to (micro-) pedoclimate
338 when assessing the earthworms' impact on soil accrual.

339

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348

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454

455 **Figure captions**

456 Figure 1: Accumulation of globular earthworm casts on soil surface in the woodland.

457 Figure 2: Weekly cast production measured in plots of 0.25 m² in woodland, shrubland and
458 meadow from July 2016 to December 2018. The red curve represents the mean of the
459 production (n=4). The grey shadow represents the standard error. The blue dashed curve
460 represents the LOESS smoothing (span = 0.2).

461 Figure 3: (a) Predicted vs. measured weekly production of earthworm casts of validation
462 dataset derived from random forest models in woodland, shrubland and meadow.
463 Abbreviation: R², coefficient of determination. RMSE, root-mean-square error. RPD, residual
464 predictive deviation. The black dashed line corresponds to y = x; (b) Relative importance of
465 predictors (%) for each climate variables using the best prediction model. Soil and air
466 temperature (S-temp and A-temp); soil water tension from 5 to 150 cm depth (5 to 150).

467 Figure 4: (a) photos depicting the formation of a new soil horizon caused by the accumulation
468 of earthworm casts after 2.5 years in plots of 0.25 m² in woodland (W), shrubland (S) and
469 meadow (M); (b) Boxplot presenting the increase in soil height after 2.5 years (height in plots
470 with casts minus height in plots without cast); (c) degradation of earthworm casts calculated
471 as the sum of the mass of casts collected every week in the four plots for 2.5 years minus the
472 mass of casts collected after 2.5 years in the four untouched plots.

473

474 Figure 5: Box plots presenting (a) runoff coefficient and (b) cumulative soil detachment
475 measured in plots of 0.25 m² with earthworm casts and without cast from the 18 of August to
476 the 27 of October 2018. The star indicates statistically significant difference at $p < 0.05$.

477 Figure 6: Mass of earthworm casts sampled in 195 points covering the catchment of 50 ha.
478 The white square represented the average mass of the different types of casts. Abbreviation:
479 wet, stand cast in production; dry, stand cast abandoned but not degraded; broken, cast not
480 stand; total, sum of all the types of casts.

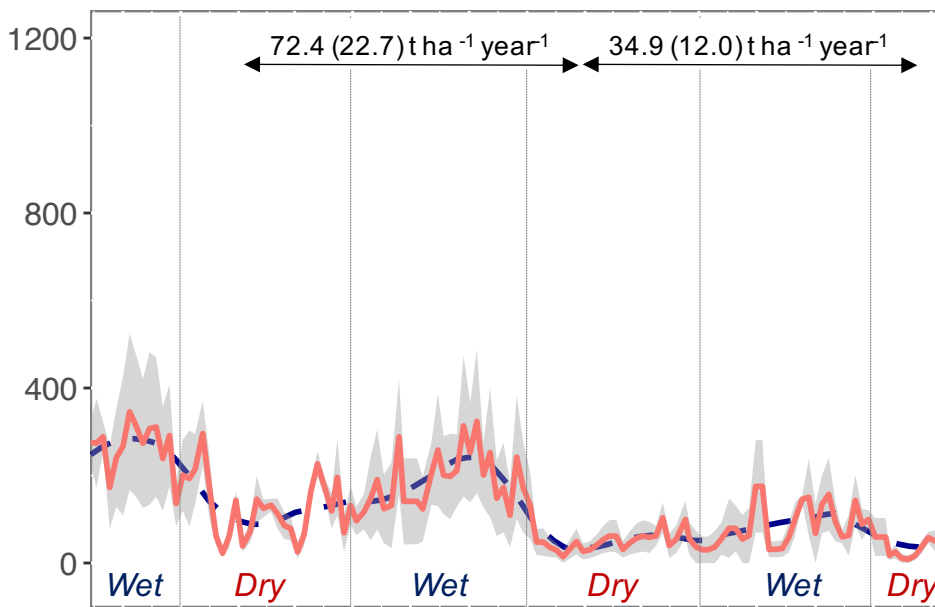
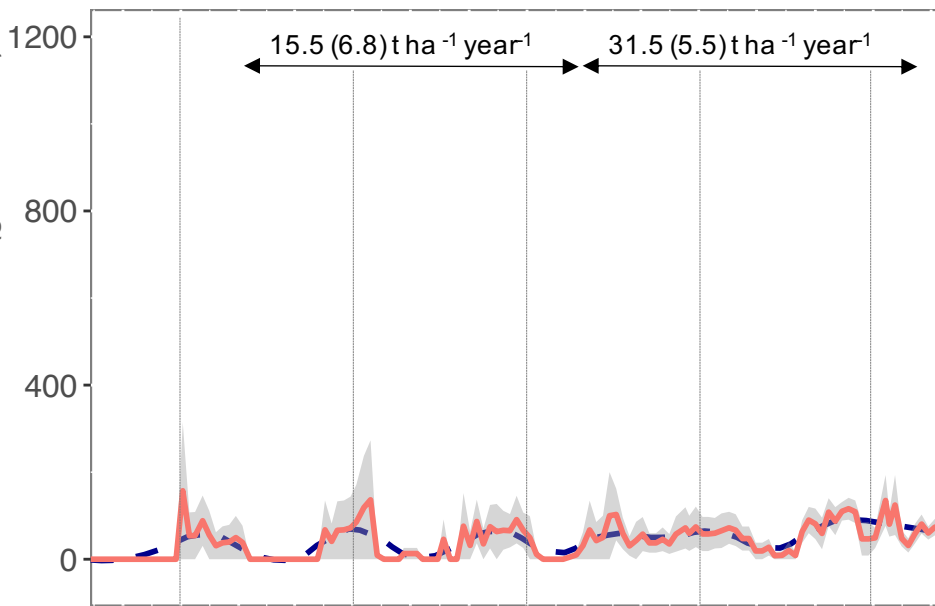
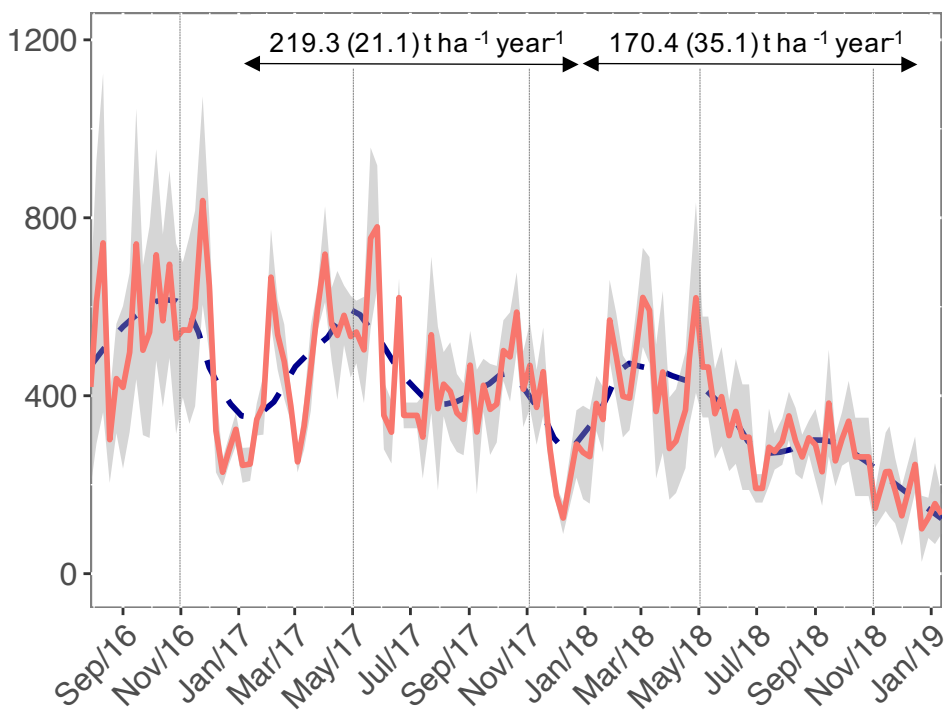
481 Figure 7: linear relationship between the number of earthworm casts collected after 1 week of
482 production in plots of 0.25 m² in February 2017 in woodland (circle), shrubland (triangle) and
483 meadow (square) and the cumulative mass of cast produced during 2017 in the same plots.

484

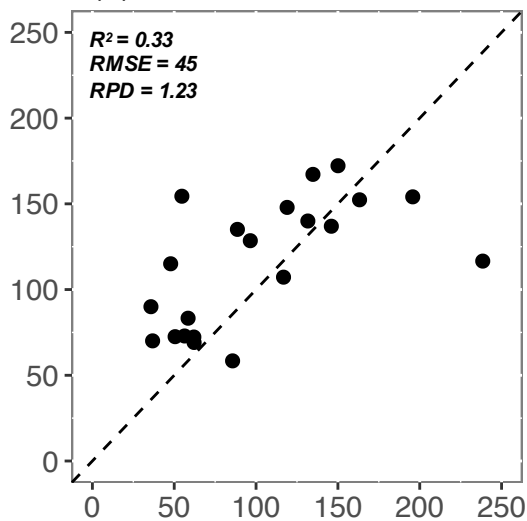


2017

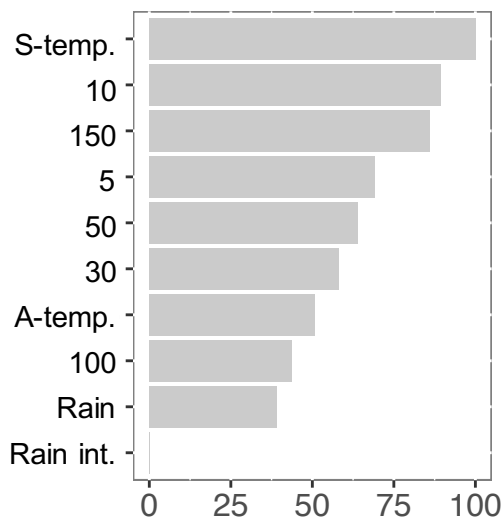
2018

**Woodland****Shrubland****Meadow**

(a)

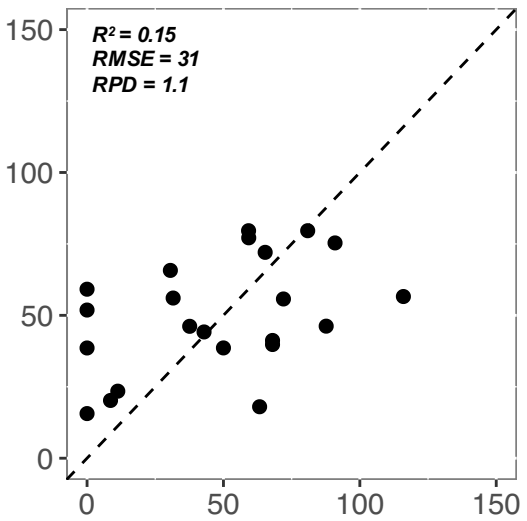


(b)

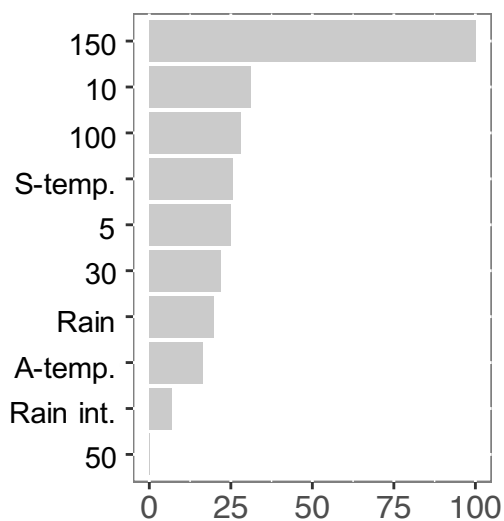


Earthworm casts predicted (g m⁻² week⁻¹)

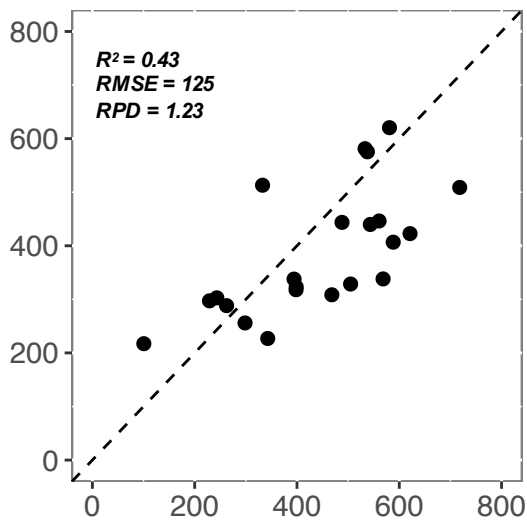
(a)



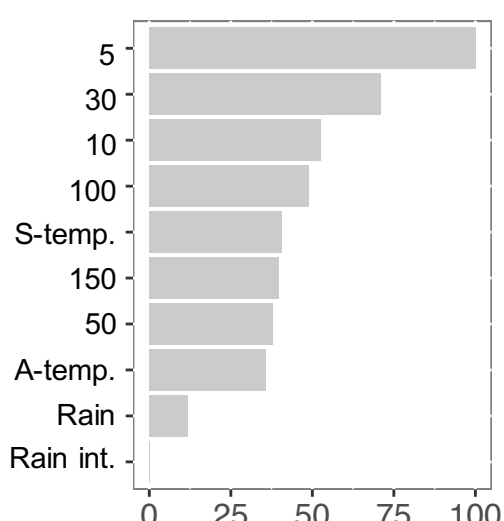
(b)



(a)



(b)



Earthworm casts measured (g m⁻² week⁻¹)

Importance

woodland

Shrubland

Meadow

(a)

woodland



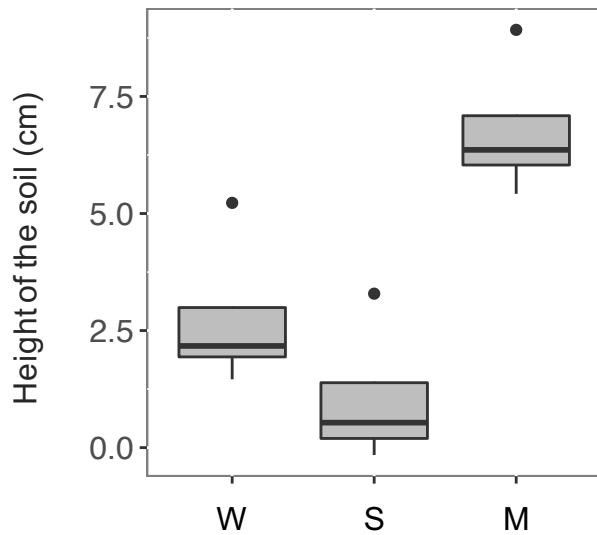
Shrubland



Meadow



(b)



(c)

