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

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Abstract

Soil is considered as a non-renewable resource, which may be lost in sloping land more rapidly than it its formed thus leading to loss of fertility and ecosystem deterioration. We hypothesized that earthworms could counteract this process due to their cast forming activity. To test this hypothesis, we quantified the production of casts in small plots of 0.25 m^2 established in three vegetation units (woodland, shrubland and meadow) in a catchment of 50 ha for 2.5 years in relation to their (micro-) pedoclimatic conditions. We also assessed their impact on water runoff and soil detachment. Moreover, we quantified the mass of casts deposited in the entire catchment on a regular grid of 50 m and we measured soil erosion at the outlet of the catchment.

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

Keywords: tropical soil, bioturbation, earthworm cast

1. Introduction

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

Surface earthworm casting activity is highly variable and reaches its record in the tropics with 250 t ha^{-1} $year^{-1}$ measured in Nigeria (Madge, 1969). Once deposited on the soil surface, casts are degraded by the rain and/or by the trampling of large animals depending on environmental and ecological factors. For instance, the production and degradation of casts is expected to be higher in tropical than in temperate environments, because of higher temperature and higher precipitations and greater biological activity. Vegetation may protect casts from destruction though raindrop impacts and extend their lifespan (Decaëns, 2000). However, based on our visual assessment in the field, we hypothesized that the casts' resistance to erosion also depends on soil properties such as their carbon and clay content or on the cast type (granular < past-like < globular) formed in different situations. If not degraded on site, casts can also contribute to the sediment load following water erosion, especially in tropical sloping land (Blanchart et al., 2004; Jouquet et al., 2010). Generally, the impact of erosion on the fate of earthworm casts was estimated from indicators, as for example soil aggregate stability to water or measured directly in the field at small scale on erosion plots under natural or simulated rainfalls (Hazelhoff et al., 1981; Jouquet et al., 2008b, 2012, 2013; Le Bayon et al., 2002; Le Bayon and Binet, 1999, 2001; Podwojewski et al., 2008; Sharpley and Syers, 1976). These approaches are not necessarily representative of the processes taking place at the landscape scale.

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

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

2. Methods

2.1. Study site

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

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

Eight plots of 0.25 m^2 were set up from July 2016 to December 2018 in each of the three representative vegetation units (woodland, shrubland and meadow) to measure the casting activity of *A. adexilis* and its impact on runoff and soil detachment. The plot location was chosen randomly in each vegetation unit to account for the field variability of earthworm casting activity. The mean slope was 24, 17 and 13 degrees in woodland, shrubland and meadow, respectively. In each vegetation unit, four plots were kept untouched, while four other plots were used to quantify the weekly production of casts. All earthworm casts were removed from plots before the beginning of the experiment.

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

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

The sampling took place in February 2017, during the dry season because of the difficulty of walking in the catchment during the rainy season. 195 points were sampled on a regular grid (50 x 50 m) covering the entire catchment. At each point, on three replicates of 1 m^2, casts were classified into three groups (i) active (standing and wet); (ii) non-active (stand and dry) and (iii) degraded (dry and broken). The number of active and non-active casts was quantified and the weight of the three categories was determined in the field and corrected for moisture, which was determined on subsamples dried in the oven at 105°C during 24h.

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

An automatic weather station measuring on a one-minute basis the temperature and precipitation was located at the bottom of the catchment. Soil temperature sensors were buried at 10 cm depth and watermark sensors were buried at 5, 10, 30, 50, 100, 150 cm depth to continuously monitor soil temperature and soil water tension (0- 250 cm) in the three vegetation units.

2.6. Statistical analyses

One-way ANOVA and repeated measures ANOVA were performed to test the effect of the vegetation unit and the sampling time on the production of casts in the 0.25 m^2 plots, respectively. T-test was used to test the effect of presence or absence of earthworm casts on water runoff and soil detachment in 0.25 m^2 plots for each vegetation unit. Prior to running ANOVA and T-test, data were tested for homogeneity of variances and normality. Differences among treatments were declared significant at the 0.05 probability level. Between-class analysis (BCA) and Monte Carlo permutation tests (1000 permutations) was carried out to discriminate the three vegetation units in 2017 and 2018 in function of soil and air temperature and water tension. BCA measures the amount of variance restricted to the grouping factor as a percentage of the total inertia (Dray et al., 2011). Random forest regression was used to identify climatic variables influencing cast production in each vegetation unit. Random forest is a nonparametric method, which consists of a large number of individual tree models trained from bootstrap samples of the data (Breiman, 2001). The results of all individual trees are aggregated to make a single prediction. The variables tested in were total precipitations, precipitations > 20 mm h^{-1}, air temperature, soil temperature and soil water tension from 10 to 150 cm depth. The dataset for each vegetation unit represented 115 measurements of cast production and was randomly split into calibration dataset (80%) and validation dataset (20%). The optimization of parameters for the final models was based on minimizing the root mean square error (RMSE) between the measured and the estimated value of the production of casts for the calibration dataset based on 10-fold repeated cross-validation with five repetitions. The number of variables for each tree (mtry) and the number of trees in the forest (ntree) are two user-defined parameters which need to be optimized. The number of trees (ntree) was 1000 in this study. Mtry was identified as those returning the lowest RMSE by iterating mtry values from 1 to 11 representing the number of predictors. The relative importance of variables was estimated from the mean decrease in predictive accuracy. The model performances for prediction of the production of casts on the test dataset were evaluated using coefficient of determination (R^2), root mean square error of prediction (RMSE) and residual predictive deviation (RPD). The RPD denotes the ratio of the standard deviation of the measured cast production to the RMSE calculated between the measured and predicted cast production.

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

3. Results

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

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

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

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

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

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

Cast production in the entire catchment was evaluated in February 2017. The mass of casts found in the catchment varied from 0 to 6.5 kg m^{-2} and represented on average 7.5 t ha^{-1} (Fig. 6). 80% of the casts showed a degraded aspect. The number of active and non-active casts varied between 0-13 and 0-14 per m^2, respectively. The number of casts collected in 0.25 m^2 plots after one week of production in February 2017 varied between 0 to 20 per m^{-2} and was positively related ($R^2 = 0.90$) to the total mass of casts collected during the year (Fig. 7). Using this relationship for assessing the annual mass of casts produced in the entire catchment with the number of active casts, we predicted that the cast production amounted on average to 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 5 times higher than the cast mass observed on average at catchment scale (see above) and 12 times higher than the annual erosion rate measured at the outlet of the catchment, which represented only 3 t ha^{-1}.

4. Discussion

4.1. Earthworm cast production varies in space and time

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

In the shrubland and meadow, a decrease of activity was also recorded in July, when the air temperature and rainfall were highest. Since the pedoclimatic conditions were similar for the three vegetation units during the wet season, discrepancies might be linked to microclimatic variations affecting the degradation casts at the three sites. While earthworm casts after drying exhibit high aggregate stability as compared to physical soil aggregates (Jouquet et a., 2008), recently formed casts are relatively unstable (Le Mer et al., 2021) and may be degraded by rainfall impact. In fact, casts were fully exposed to high intensity precipitations in shrubland and meadow, whereas in woodland they were partly protected by the tree canopy. From 2017 to 2018, we measured lower cast production in woodland (by 50%) and meadow (by 20%). This may be partly explained by cast disintegration by rainfall impact, since the precipitations were higher by 454 mm in 2018 as compared to 2017. Moreover, contrasting impacts of precipitation events on earthworm abundance and activity under the three vegetation units cannot be excluded.

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

4.2. Earthworms generate more topsoil than they contribute to erosion

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

At the catchment scale, the mass of casts reached at several locations large amounts of up to 6.5 kg m^{-2}. This led to the formation of a vermic horizon as it was observed in the 0.25 m^2 plots under all three vegetation units. However, the high percentage of broken casts covering the soil indicated that casts were rapidly degraded. Several factors might be involved such as the raindrop impacts, the trampling of buffalo and the activity of soil organisms. We assessed by a linear relationship, that for 2017, the amount of casts produced in the catchment was 5 times higher than what we measured during the survey in February in 2017. This indicates that up to 79% of all cast produced may be degraded within one year. If all the degraded materials were washed away contributing to material leaving the catchment, the annual erosion rate would have been much higher than 3 t ha^{-1}. Therefore, we assume that the material composing earthworm casts remained within the catchment after their degradation.

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

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Figure captions

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

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

Figure 3: (a) Predicted vs. measured weekly production of earthworm casts of validation dataset derived from random forest models in woodland, shrubland and meadow. Abbreviation: R^2, coefficient of determination. RMSE, root-mean-square error. RPD, residual predictive deviation. The black dashed line corresponds to y = x; (b) Relative importance of predictors (%) for each climate variables using the best prediction model. Soil and air temperature (S-temp and A-temp); soil water tension from 5 to 150 cm depth (5 to 150).

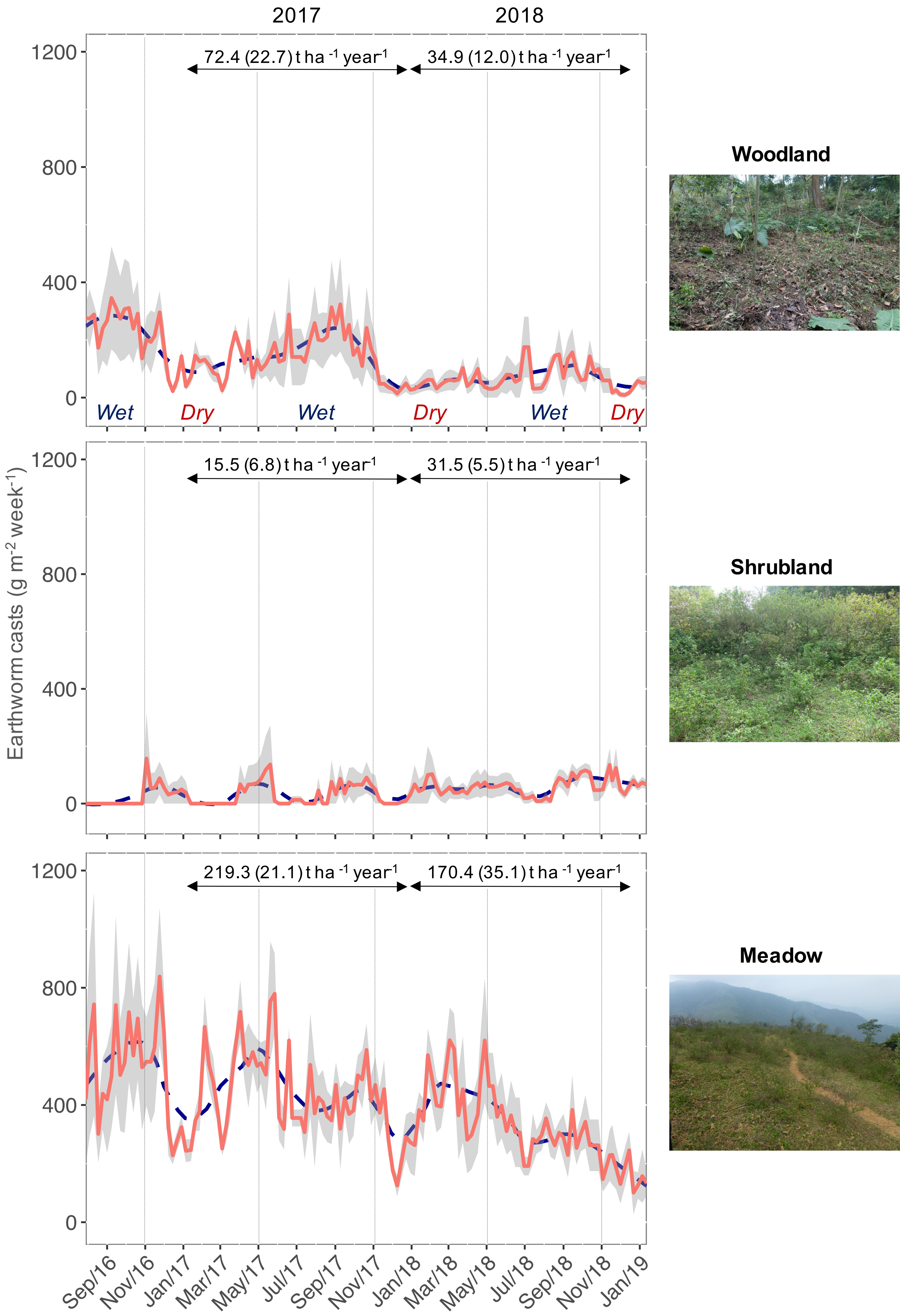
Figure 4: (a) photos depicting the formation of a new soil horizon caused by the accumulation of earthworm casts after 2.5 years in plots of 0.25 m^2 in woodland (W), shrubland (S) and meadow (M); (b) Boxplot presenting the increase in soil height after 2.5 years (height in plots with casts minus height in plots without cast); (c) degradation of earthworm casts calculated as the sum of the mass of casts collected every week in the four plots for 2.5 years minus the mass of casts collected after 2.5 years in the four untouched plots.

Figure 5: Box plots presenting (a) runoff coefficient and (b) cumulative soil detachment measured in plots of 0.25 m^2 with earthworm casts and without cast from the 18 of August to the 27 of October 2018. The star indicates statistically significant difference at $p < 0.05$.

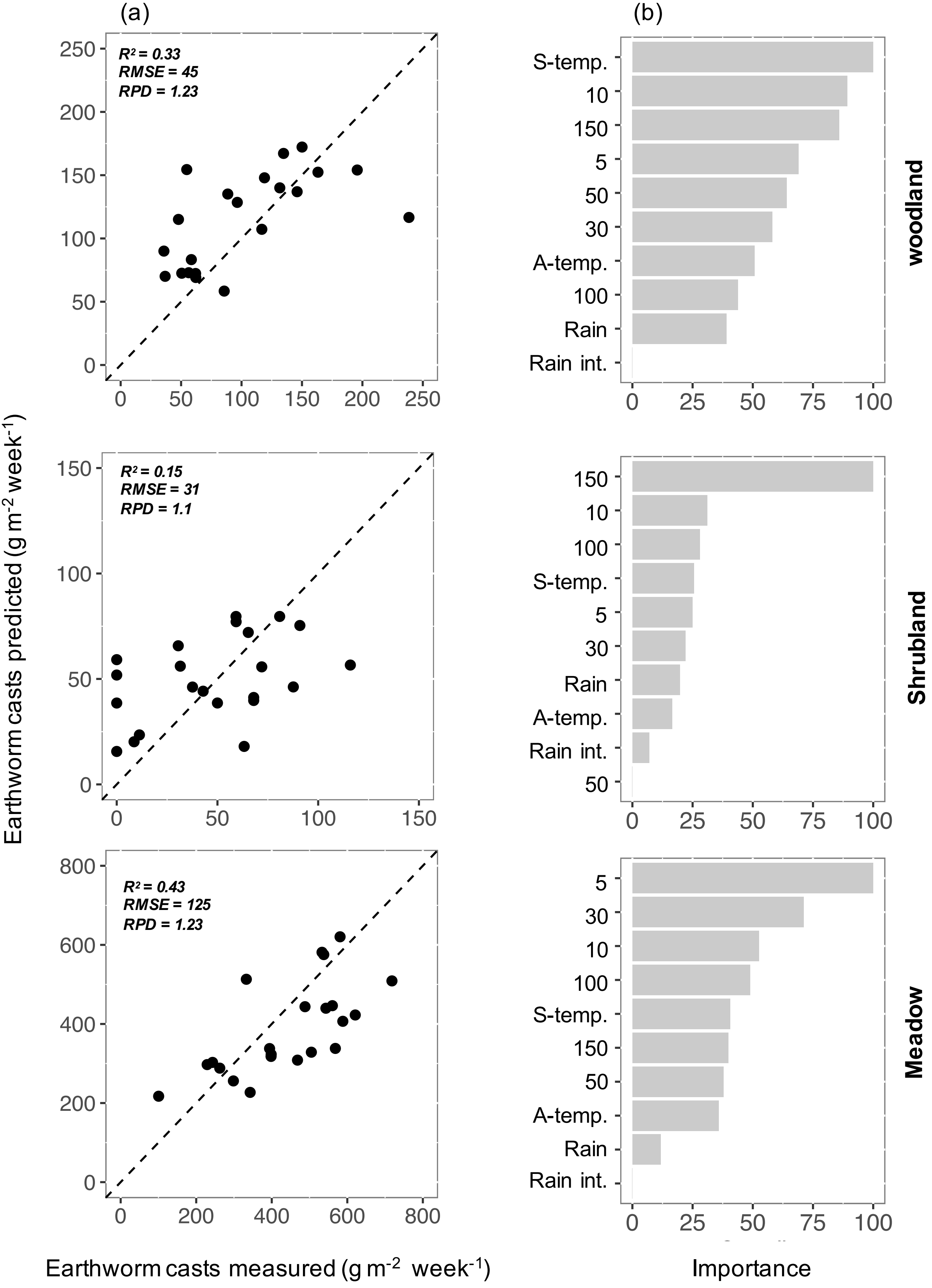
Figure 6: Mass of earthworm casts sampled in 195 points covering the catchment of 50 ha. The white square represented the average mass of the different types of casts. Abbreviation: wet, stand cast in production; dry, stand cast abandoned but not degraded; broken, cast not stand; total, sum of all the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

Figure 7: linear relationship between the number of earthworm casts collected after 1 week of production in plots of 0.25 m^2 in February 2017 in woodland (circle), shrubland (triangle) and meadow (square) and the cumulative mass of cast produced during 2017 in the same plots.

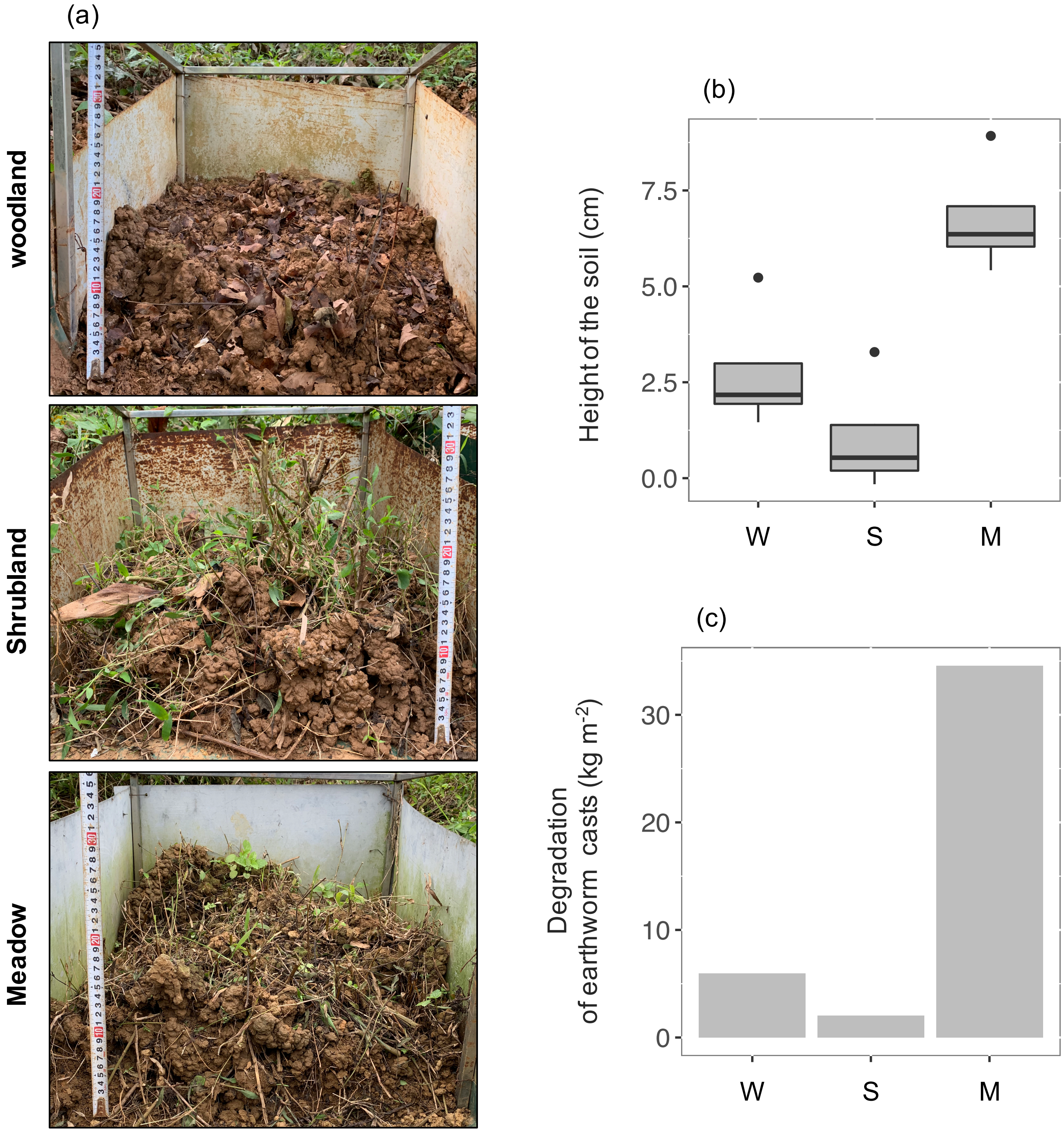

0 1 2 3 4
Nicolas Bottinelli

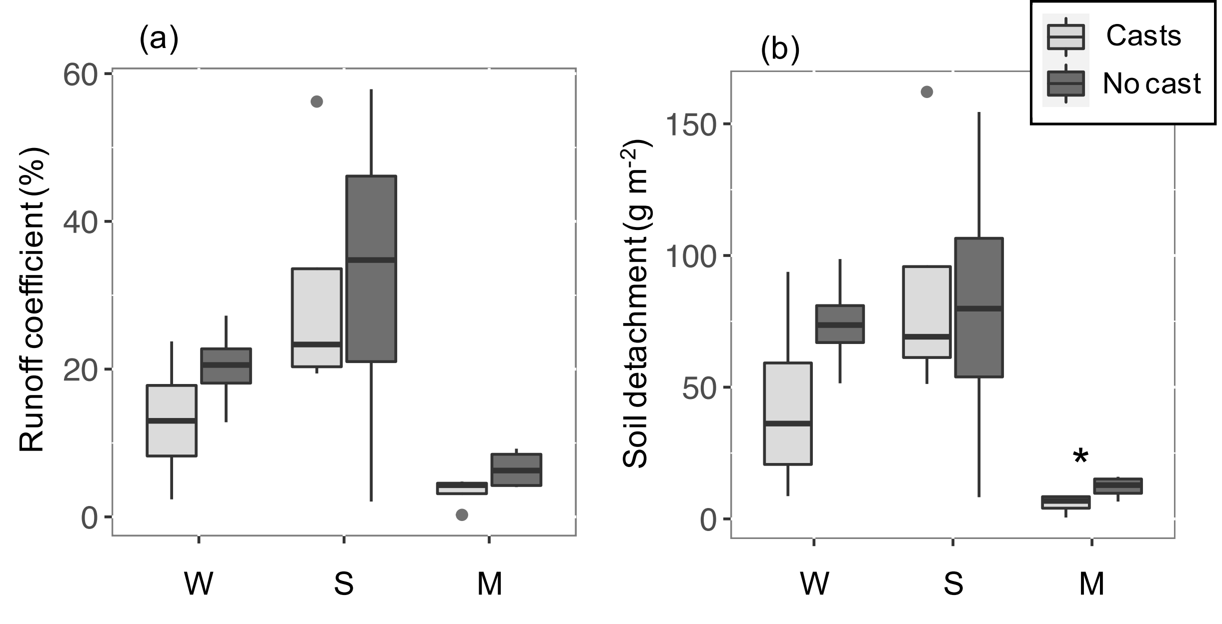


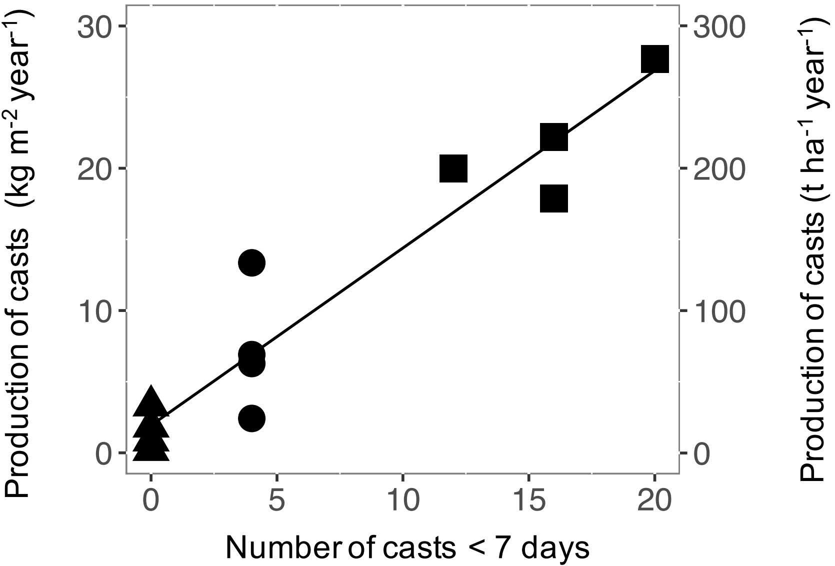
2017
2018
72.4 (22.7) t ha -1 year-1
34.9 (12.0) t ha -1 year-1
Wet
Dry
Wet
Dry
Wet
Dry
Woodland
15.5 (6.8) t ha -1 year-1
31.5 (5.5) t ha -1 year-1
Shrubland
219.3 (21.1) t ha -1 year-1
170.4 (35.1) t ha -1 year-1
Meadow
Earthworm casts (g m-2 week-1)
1200
800
400
0
Sep/16
Nov/16
Jan/17
Mar/17
May/17
Jul/17
Sep/17
Nov/17
Jan/18
Mar/18
May/18
Jul/18
Sep/18
Nov/18
Jan/19



(a)
(b)
R² = 0.33
RMSE = 45
RPD = 1.23
S-temp.
10
150
5
50
30
A-temp.
100
Rain
Rain int.
woodland
R² = 0.15
RMSE = 31
RPD = 1.1
150
10
100
S-temp.
5
30
Rain
A-temp.
Rain int.
50
Shrubland
R² = 0.43
RMSE = 125
RPD = 1.23
5
30
10
100
S-temp.
150
50
A-temp.
Rain
Rain int.
Meadow
Earthworm casts predicted (g m-2 week-1)
Earthworm casts measured (g m-2 week-1)
Importance


(a)
woodland
Shrubland
Meadow
(b)
Height of the soil (cm)
7.5
5.0
2.5
0.0
W
S
M
(c)
Degradation
of earthworm casts (kg m-2)
30
20
10
0
W
S
M


(a)
(b)
Runoff coefficient (%)
60
40
20
0
W
S
M
Soil detachment (g m-2)
150
100
50
0
W
S
M
*
Casts
No cast


Production of casts (kg m^{-2} year^{-1})
Production of casts (t ha^{-1} year^{-1})
Number of casts < 7 days
0
10
20
30
0
100
200
300
0
5
10
15
20