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## Shallow landslides as drivers for slope ecosystem evolution and biophysical diversity

**Abstract** Shallow landslides may be seen as local disturbances that foster the evolution of slope landscapes as part of their self-regulating capacity. Gaining insight into how slope ecosystems function and evolve could make eco-engineering interventions on slopes more successful. The objective of the present study is to detect traits of shallow landslide-triggered ecosystem evolution, self-regulation and biophysical diversity in a small-scale landslide-prone slope in Northeast Scotland. A protocol was defined to explore the emergence of landslide-driven slope habitats. This protocol studied plant diversity, species richness and plant biomass differences and their interactions with certain soil and topographic attributes at three slope strata during two consecutive growing seasons following an assemblage of shallow landslide events. Plant species and soil properties with potential as indicators of the different landslide-driven slope habitats and landscape evolution were also considered. Shallow landslides contributed to biophysical diversity and created distinct slope habitats within the landscape. Habitat differences in terms of species richness and composition were a direct consequence of the slope self-regulation. Certain plant species were found to be valid indicators of landslide-driven biophysical diversity. Soil total nitrogen and resistance to penetration were related to slope habitat and landscape evolution. As expected, plant establishment relied upon light and nitrogen trade-offs, which in turn were influenced by landscape topography. The insights derived from this study will be useful in slope restoration, particularly in harmonising effective actions with the functioning of landslide-prone ecosystems. Further research directions to clarify the observed variability and interactions are highlighted.

**Keywords** Shallow landslide · Ecosystem · Self-organisation · Plant diversity · Biophysical diversity · Slope restoration

### Introduction

Landslides are normally seen as catastrophic geomorphological processes that lead to dramatic losses of soil, human property and life globally. However, from an ecological perspective, they are natural disturbance episodes of varying frequency and intensity that contribute to the natural evolution of sloped ecosystems (Walker and Shield 2013). The ecology of landslides has been relatively well studied (see Walker and Shield 2013 for review), but it is still an emergent discipline. During a landslide, nutrient-rich soil materials usually move downwards due to the action of gravity (Guariguata 1990; Walker et al. 1996). This leads to the differentiation of clear slope zones on the basis of the accumulation of soil materials (Velázquez and Gómez-Sal 2008; Elias and Dias 2009; Walker et al. 2009; Neto et al. 2017). Additionally, the biophysical diversity of the landslide-prone landscape increases (Geertsema and Pojar 2007) due to marked changes that can occur in soil properties and vegetation cover (Shiels et al. 2008; Elias and Dias 2009) and the emergence of novel topographical shapes (Cendrero and Dramis 1996).

Shallow landslides increase the openness (Odum 1969) of the landscape by displacing the topsoil and established vegetation downwards on the slope at the time of failure (Walker et al. 1996). This is evident in the bare scars and patches produced after landslides. These landscape gaps present unique ecological features (e.g. areas with low levels of light competition between plant individuals; Walker et al. 1996; Myster and Walker 1997) for colonisation by plants present within the surrounding landscape (Velázquez and Gómez-Sal 2008). Thus, a given slope will tend to self-organise after a landslide (Walker et al. 1996) and the most visible evidence of this can be found in a slope's re-colonisation by vegetation (Velázquez and Gómez-Sal 2008) and its subsequent succession (Myster and Walker 1997; Walker et al. 2010). These processes tend to be mimicked in human-driven slope restoration actions (e.g. Norris et al. 2008), but the process of slope self-regulation after failure and ecological factors leading to successful slope restoration (other than soil-root reinforcement; e.g. Stokes et al. 2008) need further exploration (Restrepo et al. 2009). Moreover, there is a need to establish simple and effective protocols capable of capturing the biophysical diversity and self-organisation triggered by landslides while providing interpretable and useful information for slope restoration.

Post-landslide self-organisation processes depend on the emergent biophysical heterogeneity within slope ecosystems (Velázquez and Gómez-Sal 2007). Knowledge about landslide-derived biophysical diversity may improve the success of slope restoration actions using vegetation (Walker et al. 2009). For example, insight related to the post-disturbance emergence of distinct slope zones, or habitats (Velázquez and Gómez-Sal 2008; Neto et al. 2017), and the associated colonising plants may aid in the choice of different restoration strategies within the same slope. Insight related to the environmental factors governing post-slide plant diversity, succession and establishment may provide useful information to landslide engineers and restoration ecologists in order to achieve the goals of slope restoration actions (e.g. diverse plant cover, dense plant cover, etc.) or to monitor the subsequent slope evolution. However, plant interactions with the post-landslide abiotic slope features must be clarified to enhance the slope restoration success. These interactions are not yet entirely understood (Rajaniemi et al. 2003; Restrepo et al. 2009), and tools to adequately detect and interpret them are needed.

Plant-environment relationships can be complex. For example, plants need to compensate for dramatic differences in resource (i.e. energy, water and nutrients) availability across the environment in order to thrive (Chapin et al. 1987; Herbert et al. 2004). In particular, trade-offs between light and nitrogen seem to be the key controls in the establishment of plant communities after disturbance (Walters and Reich 1997; Myster and Walker 1997; Soto et al. 2017). Nitrogen-rich soils tend to foster the production of plant aboveground biomass (Urbano 1995). This may enhance the ability of vegetation to intercept light (Wilson and Tilman 1995; Walters and Reich 1997), but it also may promote plant

competition for aboveground resources such as light (Rajaniemi et al. 2003; Herbert et al. 2004), leading to shifts in the composition and diversity of plant communities (e.g. Wilson and Tilman 1995). Light and nitrogen availability may be governed by landslide dynamics, but also by the landscape topography (e.g. Franklin 1995; Hood et al. 2003; Wang et al. 2015). For instance, slope orientation (i.e. aspect or azimuth) will determine the amount of incoming energy (e.g. Gallardo-Cruz et al. 2009), which in turn will affect photosynthesis, evapotranspiration, soil temperature and soil moisture content—all crucial variables for plant development. Slope surface curvature affects plant performance (e.g. Moeslund et al. 2013) by its influence on subsurface water flow, litter accumulation and soil erosion/deposition rates which, in turn, are related to soil depth and texture, water holding capacity and nutrient availability (Heimsath et al. 1997). A slope gradient greater than 45° will hinder the establishment of vegetation (Bochet and Garcia-Fayos 2004), in part not only because such slope will be prone to instability (i.e. more frequent disturbance; Velázquez and Gómez-Sal 2008; Lu and Godt 2013), but also because the nutrients will likely be washed down from steeper zones and accumulate in flatter areas (Heimsath et al. 1997; Hood et al. 2003; Bertoldi et al. 2006).

The study of the complex interactions between plants and their environment requires the use of advanced statistical tools (e.g. principal component analysis; Borcard et al. 2011). As indicated earlier, the challenge includes the need to clarify and interpret the results of statistical analyses to provide understandable and practical information to landslide engineers and restoration ecologists. The advent of machine learning techniques, such as regression trees (Breiman et al. 1984), may aid in the interpretation of complex interactions between plants and their environment (e.g. Kallimanis et al. 2007; Revermann et al. 2016). Regression trees have four major benefits: (1) They are more powerful than classical multiple regressions (as the relationship between response and predictor variables is not prespecified), (2) they can effectively model the change in direction of the effect of one factor in

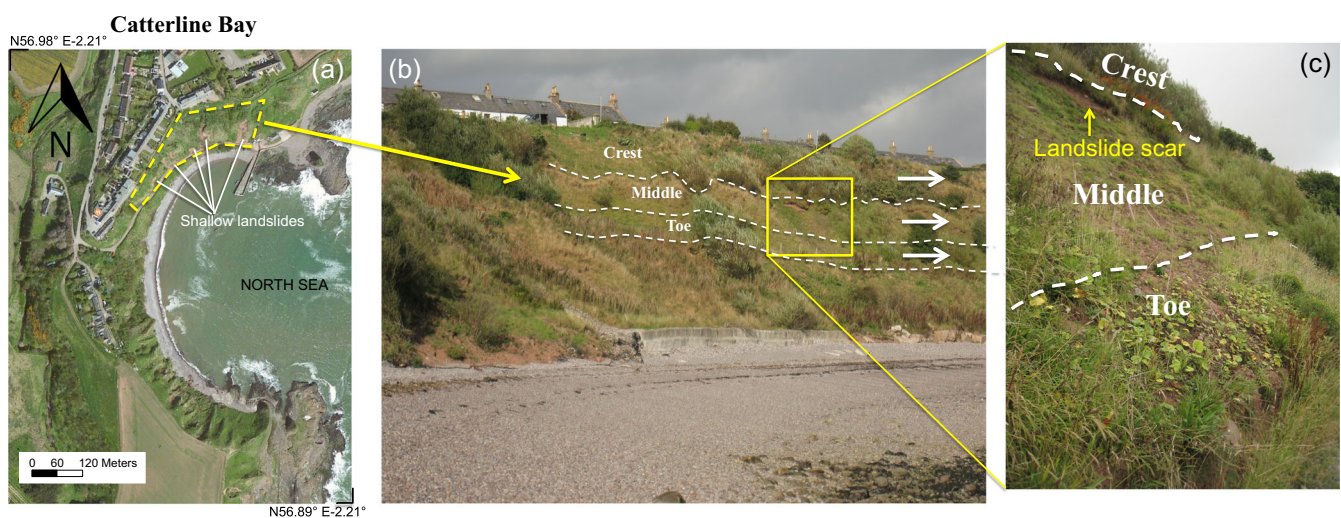
response to the levels of another factor, (3) they are more interpretable than the commonly used ordination techniques, and (4) they are able to depict the hierarchical structure by which ecosystems are built (Jørgensen 2007).

The goal of this study is to detect early traits of landslide-triggered ecosystem evolution, self-regulation and biophysical diversity in a small-scale landslide-prone coastal slope in Northeast Scotland. To achieve this, a novel protocol was defined for exploring the emergence of landslide-driven slope habitats. Plant diversity, species richness and plant biomass differences together with their interactions with certain soil and topographic attributes at three different slope strata are studied during two consecutive growing seasons following an assemblage of shallow landslide episodes. The protocol also assesses potential plant indicator species for the different landslide-driven slope habitats and studies soil properties indicative of slope habitat and landscape evolution. In the light of the findings and observations, recommendations related to slope restoration actions are proposed.

## Materials and methods

### Study site

Plant and biophysical diversity were studied on an accessible section of a landslide-prone slope during two consecutive growing seasons (2014 and 2015) following an assemblage of shallow landslide events. The slope is located adjacent to Catterline Bay, Northeast Scotland, UK (WGS84 Long -2.21 Lat 56.90; Fig. 1a), where multiple small-scale shallow landslides (ca. 100–300 m<sup>2</sup>; Fig. 1a) occurred in April 2013 (Kincardineshire Observer 11/4/2013) as a result of a period of prolonged rainfall. Consequently, a number of failure zones appeared distributed close to each other (i.e. less than ca. 10 m apart) across the studied slope (Fig. 1a); their scars were easily identifiable as exposed bare ground or areas of sparse vegetation. The surveyed section of the slope was mainly vegetated with early successional plant communities (i.e. herbs and grasses; Fig. 1b, c) surrounded by a mixture of



**Fig. 1** a Study site location and area of study (dashed frame). White lines indicate the location of shallow landslides occurring in April 2013. b Slope strata (i.e. crest, middle and toe) and sampling direction within each stratum (white arrows). c Section of the studied slope where the different slope strata are indicated. Aerial image source: GetMapping (2014)

areas dominated by herbaceous weeds and grasses, riparian trees and shrubs (e.g. willow, sycamore, ash, hawthorn) and agricultural crops of wheat and barley.

The study site has a mean annual temperature of 8.0 °C and mean annual rainfall of 1232 mm (UK Met Office 2015), characteristic of a humid temperate climate site (Cfc: subpolar oceanic climate; Köppen 1884). The topography of the site is dominated by sloped (25–50°) terrain and cliffs running into the North Sea (Fig. 1), where often shallow (ca. <2 m), silty sand soils (sand 79.82%; silt 5.85%; clay 3.08%; BS 1377-2: 1990) can be found resting on sedimentary bedrock (i.e. conglomerate; BGS 1999). Overall, the studied slope is facing east, southeast and south directions (Fig. 1a).

### Sampling approach

The studied slope was divided prior to sampling into three slope strata of similar width—i.e. crest (*c*), middle (*m*) and toe (*t*) (Fig. 1b, c). The criteria employed to stratify the slope were the accumulation of slope-forming materials following landslides and the recurrence of shallow landslide (i.e. disturbance) events. The feature used to delineate the strata was the presence or absence of landslide scars (Fig. 1c). The middle and toe strata (Fig. 1b, c) were delineated as the initiation and deposition zones, respectively, of the shallow landslides occurring in April 2013. The middle stratum was delimited from the toe for presenting visible landslide scars (Fig. 1c). The crest stratum, comprising the top part of the studied slope (Fig. 1c, d), remained stable during the 2013 landslide episode and has been disturbance-free for a longer time. This can be seen from the absence of landslide scars and from the establishment of dense patches of shrub species such as gorse, hawthorn and willow in some zones (Fig. 1b, c).

A stratified haphazard sampling design (e.g. Hall et al. 2013) was implemented to collect vegetation samples within each predefined slope stratum at the apices of the 2014 and 2015 growing seasons (i.e. mid-July). A 1-m buffer zone from each boundary was delimited within each stratum to avoid edge effects upon sampling. The vegetation samples were obtained by using a 0.5-m<sup>2</sup> (1.0 m × 0.5 m) aluminium frame (Fig. 2a). This was placed with the long side facing the top of the landslide (Myster and Walker 1997) on locations (i.e. sampling units or quadrats) chosen by throwing the aluminium frame aimlessly within each slope stratum. The quadrats were spaced approximately 10 m from each other along the direction of the contour lines within each slope

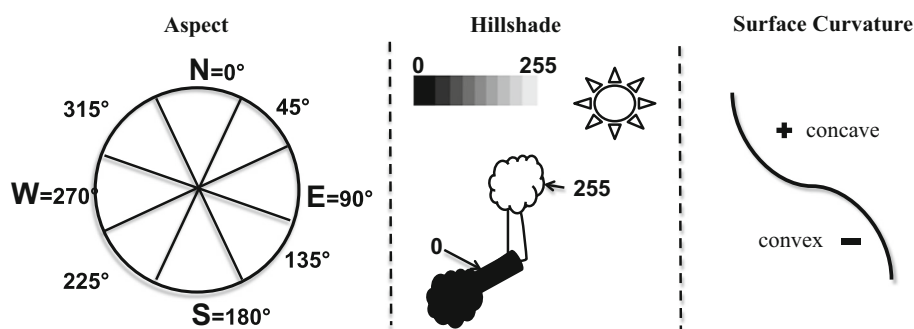
stratum (Fig. 1b), ensuring an adequate spatial coverage of the studied slope. The whole slope section annotated in Fig. 1a was sampled, as landslide scars were observed throughout. All of the plant material found within the aluminium frame (i.e. quadrat) was clipped to the ground surface (USDA-NRCS 1997) using a sickle. The harvested vegetation was tied into bundles and transported to the laboratory for further processing (see “Plant identification, dry biomass determination and species abundance” section). In total, 59 quadrats were surveyed: 25 in 2014 (*c* = 8; *m* = 8; *t* = 9) and 34 in 2015 (*c* = 12; *m* = 9; *t* = 13).

The geographical position of each quadrat was recorded with a Garmin Monterra™ GPS. Soil samples were collected with a core auger from each quadrat at a depth ranging between 0 and 15 cm below the ground level (b.g.l.) for determination of soil organic matter (SOM; Lost on Ignition Method; Schulte 1996) and soil total Kjeldahl nitrogen (TKN; Bremner 1965). The soil resistance to penetration (SRP; kPa) was measured at each quadrat with a static cone penetrometer (60° vertex angled cone; 1.5-cm<sup>2</sup> basal cone area; BS 1377-4: 1990) at four different soil depths (i.e. 0, 15, 30 and 40 cm b.g.l.), from which the mean soil SRP was obtained. Each soil depth was reached by carefully removing the overlaying soil with a soil core auger, before pushing the cone into the soil up to its base and reading the stress (i.e. SRP) from the dial gauge.

The slope gradient of each quadrat was measured with a hand inclinometer while the topographic attributes aspect, hillshade (azimuth: east—i.e. morning sun position, when clear skies were more frequent during the sampling period; solar angle 45°—i.e. mean solar angle during the sampling period) and profile curvature (Fig. 2) were retrieved from a high-resolution (point spacing 2 × 2 m), photogrammetrically derived digital surface model (GetMapping 2014) using the recorded GPS coordinate points. The topographic attributes were used for analysis of the effects of topography on plant diversity metrics (see “Plant diversity metric determination” and “Environmental covariate effect on plant diversity, species richness and biomass” sections).

### Plant identification, dry biomass determination and species abundance

The plant material (vascular plants only) harvested in each bundle (see “Sampling approach” section) was separated by hand into species for subsequent identification. The identification process was carried out to the family and species level using a plant identification key (Bonnier and De Layens 2002) and the Atlas of the British and Irish flora (BRC 2016). The vegetation remnants



**Fig. 2** Explanatory illustration for the topographic attributes. Aspect or azimuth is the compass direction that the slope faces. Hillshade is derived from the aspect and determines which areas of the terrain are shaded in relation to a predefined position and inclination of the sun. A higher hillshade value refers to more sun exposure. The surface curvature is the amount by which the terrain surface deviates from being flat, acquiring a positive value when concave and negative when convex



that could not be classified (e.g. remains of grass, herbs leaf and litter) were pooled together and labelled as mixed biomass. All plant material was placed on aluminium trays tagged with the species and location and oven-dried at 70 °C for 48 h, after which the vegetation dry biomass was recorded using a digital scale ( $\pm 0.1$  g). The species abundance (Ab; %) at each quadrat was then calculated as the percentage of dry biomass of a given species with respect to the total biomass within a given quadrant (i.e. sample unit), including the mixed biomass.

#### Plant diversity metric determination

Plant diversity was assessed by estimating the Shannon-Wiener index ( $H' = -\sum_{i=1}^S p_i \ln p_i$ ;  $p_i$ : proportion of biomass belonging to the  $i$ th species;  $S$ : total number of species; Shannon and Weaver 1964) and Pielou's evenness ( $J' = H'/H'_{\max}$ ; Mulder et al. 2004) and by computing the cumulative and average species richness (i.e.  $\alpha$ -diversity; Magurran 2004) for the three considered slope strata (i.e. crest, middle, toe). To do so, species presence-absence contingency tables (i.e. incidence matrix; e.g. Gotelli and Chao 2013) were built for computing  $H'$  and species richness with the packages 'vegan' (Oksanen et al. 2016) and 'rich' (Rossi 2011), respectively, in the statistical software R 3.2.1 (R Core Team 2015). The cumulative species richness ( $S$ ) was computed as the cumulative richness encountered over the quadrats belonging to a given slope stratum and sampling year. Species richness per unit area ( $S_a$ ) was obtained by dividing  $S$  over the total sampled area per slope stratum and year (i.e. number of quadrats  $\times$  0.5 m<sup>2</sup>; see "Sampling approach" section). The average species richness ( $S_{av}$ ) was estimated as the mean richness over the sampled quadrats per stratum and year. To explore stratum differences in terms of species richness and assess consistency of sampling effort, sample-based rarefaction curves (Gotelli and Colwell 2011; Chao and Jost 2012) were implemented by plotting cumulative randomised species richness against bootstrapped (Efron 1979) sampling intensity for the three evaluated strata with the R package rich (Rossi 2011).

#### Differences between slope strata

Slope strata differences in terms of plant diversity (i.e.  $H'$  and  $J'$ ) were quantified using Kruskal-Wallis tests at 95 and 99% confidence levels in R 3.2.1 (R Core Team 2015). The same procedure was used to evaluate strata differences in terms of  $S_a$ , SRP, SOM, TKN and total aboveground plant dry biomass. Sampling year differences (i.e. 2014 vs. 2015) in terms of the previous variables were evaluated in the same manner. Differences in cumulative species richness were assessed by a randomisation (i.e. permutation) test (e.g. Richardson and Richards 2008) with the R package rich (Rossi 2011); this test does not control for differences in sampling effort (i.e. number of samples or sample units) between the three strata but instead returns the probability of different species richness among the compared strata. Significant differences were considered when the probability was beyond 95%. Moreover, differences in terms of the species composition and relative abundance distribution (i.e.  $\beta$ -diversity; Anderson et al. 2011) between the three considered slope strata were evaluated using the Bray-Curtis (B-C) similarity index (i.e.  $BC = 1 - \frac{2c_{ij}}{s_i + s_j}$ ;  $c_{ij}$ : number of common species between two sites  $s_i$  and  $s_j$ ; total number of species counted at both

sites; Somerfield 2008), which ranges between 0 and 1 (i.e. a B-C value of 0 denotes identical sites).

#### Indicator species analysis

Potential plant indicator species for the three considered slope strata (i.e. crest, middle, toe) were identified by estimating the indicator value (Dufrene and Legendre 1997) of each encountered plant species with the R package 'indicspecies' (De Caceres and Legendre 2009). Indicator value (IndVal) is an index related to the species abundance (Ab) that measures the association between species and a particular habitat (De Caceres 2013) or stratum. Thus, indicator value is the product of species specificity ( $A$ ) and fidelity ( $B$ ) (Dufrene and Legendre 1997), where  $A$  is the probability that the surveyed site (i.e. sampling unit) belongs to the target habitat given the fact that the species have been found there and  $B$  is the probability of finding the species in units belonging to a particular habitat. Hence, indicspecies' functions first estimate IndVal between the species and each habitat and then look for the habitat corresponding to the highest association value. The statistical significance of this relationship is tested using a randomisation (i.e. permutation) test (De Caceres 2013). Species preferences for a given slope habitat, or stratum, were also evaluated with the previous approach. Additionally, the extent that a given habitat is covered by a plant indicator was quantified by estimating coverage (De Caceres et al. 2012), which is the proportion of sampling locations belonging to a given habitat where one or another plant indicator (i.e. a species or a species combination) is found.

#### Environmental covariate effect on plant diversity, species richness and biomass

The effects of the environmental covariates (i.e. soil resistance to penetration (SRP), soil organic matter (SOM), soil total Kjeldahl nitrogen (TKN), slope gradient, hillshade, aspect and profile curvature) on plant diversity ( $H'$ ), species richness and plant dry biomass were first evaluated using Pearson's correlation test in R 2.3.1. To infer more complex and hierarchical effects of the environmental covariates and include slope stratum (i.e. factor or qualitative variable) as a predictor variable, regression trees (Breiman et al. 1984; Prasad et al. 2006) were fitted between the three considered response variables (i.e.  $H'$ , species richness and plant dry biomass) measured in each quadrat and the environmental covariates using the R package 'rpart' (Therneau et al. 2015). In total, six regression trees were implemented: two for each response variable, with one set including SRP as covariate and only considering information collected during the 2015 campaign and another set without SRP and considering information from both years (i.e. 2014 and 2015) since SRP was only measured in 2015 and may obscure the effect of other relevant attributes. Outcomes derived from regression trees were plotted as dendrograms. The position of each node (i.e. tree leaf) within the tree, or dendrogram, is the hierarchical contribution of a given predictor variable (i.e. environmental covariate) to the prediction of the response variable (i.e.  $H'$ , species richness or plant dry biomass). The terminal nodes of the dendrogram contain the mean response. The regression trees were pruned using a complexity parameter of 0.06 to avoid

overfitting, reduce the number of final nodes (e.g. Prasad et al. 2006) and enhance the clearness of the outcomes. The goodness of fit from the regression trees was evaluated with a random holdback method (i.e. the model was fitted with 70% of the original data and then validated with the 30% remaining) by estimating the coefficient of determination ( $R^2$ ) and residual mean square error (RMSE) and then plotting the objective functions between observed and predicted values (e.g. Malone 2013).

## Results

### Plant diversity, species richness and slope strata

The dominant vegetation found on the studied landslide-prone slope (Fig. 1a) comprised herbs and grasses. The undisturbed portions of the slope (i.e. stable during the last landslide event and not surveyed herein) generally presented woody vegetation species such as willow, hawthorn, sycamore and ash.

Plant diversity (Table 1; Fig. 3a), evaluated in terms of  $H'$ , ranged from 1.19 to 1.41 with a relatively high species evenness in all cases ( $J' > 0.6$ ; Table 1) and did not present significant differences between the slope strata ( $H'$ :  $\chi^2 = 0.52$ ,  $df = 2$ ,  $p = 0.77$ ;  $J'$ :  $\chi^2 = 0.52$ ,  $df = 2$ ,  $p = 0.77$ ) or the years ( $\chi^2 = 0.04$ ,  $df = 1$ ,  $p = 0.84$ ). However, the cumulative species richness ( $S$ ; i.e.  $\alpha$ -diversity; Table 1; Fig. 3b) showed an increasing trend down the slope strata gradient, with  $S$  being significantly higher ( $p < 0.05$ ) at the toe ( $t$ ) (Table 1; Fig. 3b) when compared to the crest ( $c$ ) for the 2014 campaign (Table 1; Fig. 3b). The species richness per unit area ( $S_a$ ; Table 1) did not present statistically significant differences between the strata ( $\chi^2 = 2.57$ ,  $df = 2$ ,  $p = 0.28$ ), although the middle stratum showed the highest value for both sampling campaigns (Table 1). Overall, the toe stratum had more plant species in both years, particularly not only compared to the crest stratum (11 and 6 in total, 2014 and 2015, respectively) but also compared to the middle stratum (2 and 1 in total, 2014 and 2015, respectively). In the 2015 campaign, the middle stratum had in total seven species more than the crest. The species composition differences (i.e.  $\beta$ -diversity) between the slope strata tended to be more similar for the 2014 campaign (B-C<sub>c-m</sub> 0.24; B-C<sub>c-t</sub> 0.28; B-C<sub>m-t</sub> 0.39) than for the 2015 (B-C<sub>c-m</sub> 0.40; B-C<sub>c-t</sub> 0.52; B-C<sub>m-t</sub> 0.59), with the toe stratum being the most different in both cases. On the basis of the rarefaction curves (Fig. 3b), the sampling intensity was fair for the toe and middle strata; the rarefaction curves just started to reach the asymptote. For the crest stratum, however, the asymptote was reached, indicating that species pool was well covered with the sampling intensity employed (Fig. 3b).

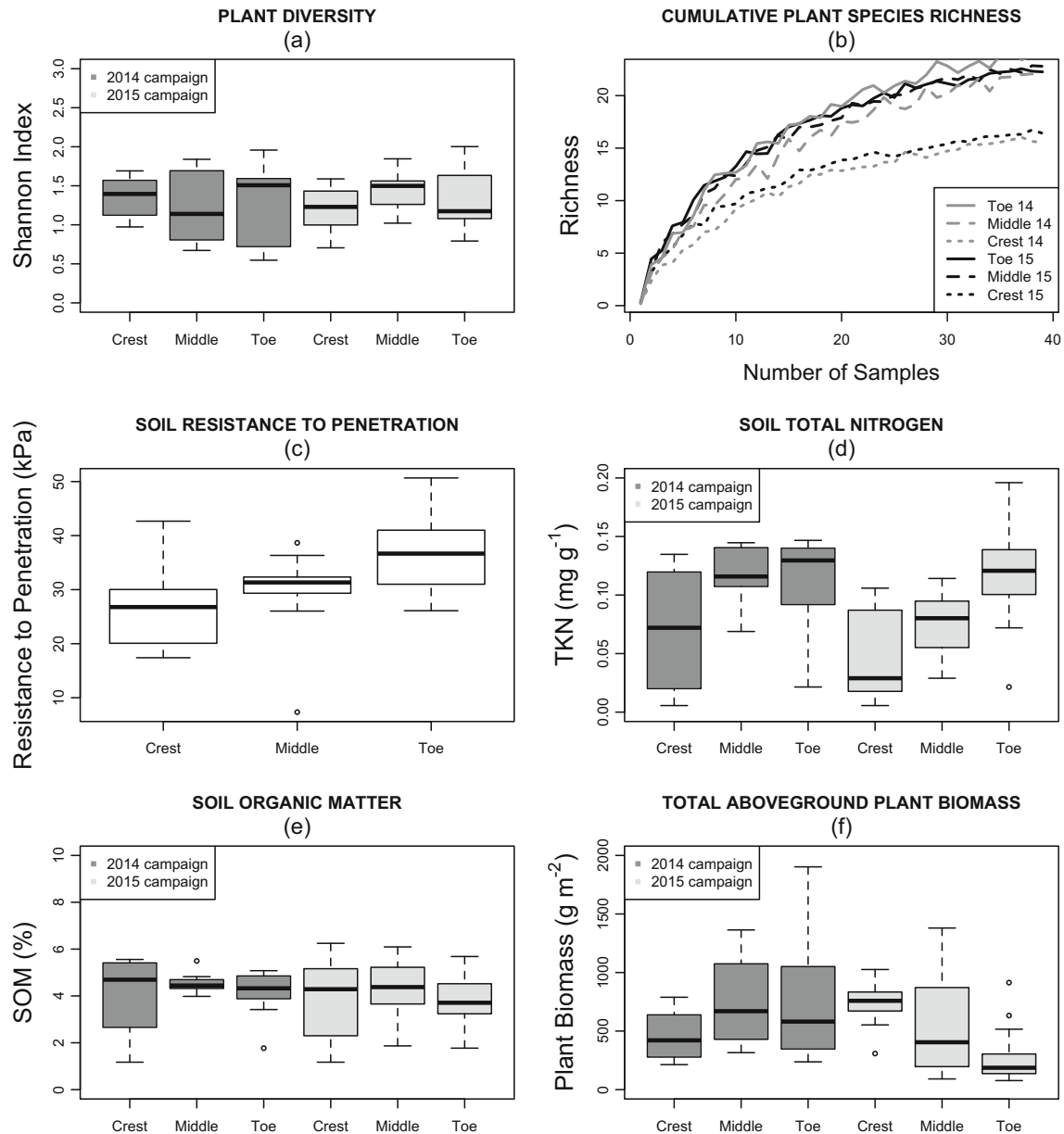
Consistent stratum differences were also encountered in terms of SRP (Table 1; Fig. 3c), which was statistically higher (i.e. higher SRP) at the toe ( $\chi^2 = 9.59$ ,  $df = 2$ ,  $p < 0.01$ ). The total soil nitrogen (TKN; Table 1; Fig. 3d) was statistically higher at the toe ( $\chi^2 = 12.16$ ,  $df = 2$ ,  $p < 0.01$ ) in 2015, although it remained relatively unchanged during the studied years ( $\chi^2 = 3.64$ ,  $df = 1$ ,  $p = 0.06$ ). Similarly, the total plant dry biomass (Table 1; Fig. 3f) was statistically higher ( $\chi^2 = 11.96$ ,  $df = 2$ ,  $p < 0.05$ ) at the crest for 2015, although no differences were found between the sampled

**Table 1** Mean values  $\pm$  standard deviation for the assessed plant diversity metrics and soil environmental covariates for the studied slope strata and field campaigns

Habitat	Season	$H'$	$J'$	$S$	$S_a$ (species m <sup>-2</sup> )	Sav	Biomass (g m <sup>-2</sup> )	SRP (kPa)	OM (%)	TKN (mg g <sup>-1</sup> )
Crest	2014	1.35 $\pm$ 0.27	0.68 $\pm$ 0.13	18	4.5	1.3 $\pm$ 2.7	460 $\pm$ 211	–	4.03 $\pm$ 1.70	0.07 $\pm$ 0.05
	2015	1.19 $\pm$ 0.29	0.59 $\pm$ 0.14	20	3.3	1.82 $\pm$ 2.81	736 $\pm$ 182*	26.39 $\pm$ 7.15	3.91 $\pm$ 1.78	0.05 $\pm$ 0.04
Middle	2014	1.22 $\pm$ 0.47	0.61 $\pm$ 0.24	27	6.75	1.59 $\pm$ 3.56	931 $\pm$ 817	–	4.55 $\pm$ 0.45	0.12 $\pm$ 0.02
	2015	1.41 $\pm$ 0.27	0.70 $\pm$ 0.14	28	6.2	1.87 $\pm$ 3.51	535 $\pm$ 442	29.30 $\pm$ 9.02	4.27 $\pm$ 1.28	0.08 $\pm$ 0.03
Toe	2014	1.32 $\pm$ 0.55	0.66 $\pm$ 0.28	29*	6.4	2.01 $\pm$ 4.06	834 $\pm$ 639	–	4.14 $\pm$ 1.04	0.11 $\pm$ 0.04
	2015	1.32 $\pm$ 0.40	0.66 $\pm$ 0.20	27	4.15	2.16 $\pm$ 3.34	292 $\pm$ 249	36.14 $\pm$ 6.93**	3.77 $\pm$ 1.14	0.11 $\pm$ 0.04**

$H'$  Shannon index,  $J'$  species evenness,  $S$  cumulative species richness over the total sampled area per stratum,  $S_a$  species richness per unit area of ground,  $Sav$  average species richness over the sampling units,  $Biomass$  aboveground plant dry biomass,  $Penetrability$  soil penetrability,  $OM$  soil organic matter,  $TKN$  soil total Kjeldahl nitrogen

\*Statistically different at 95% significance; \*\*statistically different at 99% significance



**Fig. 3** a Plant diversity boxplots indicating the variation in terms of the Shannon index ( $H'$ ) across the studied slope strata and field campaigns. b Rarefaction curves indicating the cumulative species richness for the studied slope habitats and field campaigns. c Soil resistance to penetration (SRP; kPa) boxplots indicating its variation between the studied slope strata for the 2015 field campaign. d Soil total Kjeldahl nitrogen (TKN;  $\text{mg g}^{-1}$ ) boxplots indicating its variability across the studied slope habitats and field campaigns. e Soil organic matter (SOM; %) boxplots for the studied slope habitats and field campaigns. f Total aboveground plant dry biomass ( $\text{g m}^{-2}$ ) boxplots for the studied slope habitats and field campaigns

years ( $\chi^2 = 2.08$ ,  $df = 1$ ,  $p = 0.15$ ). Conversely, the SOM did not show differences among the studied strata (SOM:  $\chi^2 = 2.05$ ,  $df = 5$ ,  $p = 0.84$ ) or the years ( $\chi^2 = 0.84$ ,  $df = 1$ ,  $p = 0.36$ ), although, in general, it showed higher levels at the crest (Fig. 3e).

#### Plant indicator species for slope habitats

The indicator species analysis detected six potential plant indicators (Table 2) out of 42 encountered plant species (i.e.  $\gamma$ -diversity) across 22 botanical families with different habitat (or stratum)

preferences (Table 3). The crest and toe presented a single species each with high specificity (i.e. A) and moderate and low fidelity (i.e. B) and high and moderate coverage, respectively (Table 2). However, the middle habitat showed four potential indicator species with very high specificity but low fidelity and, in combination, relatively high coverage (Table 2). The toe habitat presented the highest number of species (i.e. 9) that were found only within it, while the middle and crest habitats only had two specific plant species each (Table 3). The two plant species with the highest

encountered abundance over the entire study site (Fig. 1a) were *Arrhenatherum elatius* (Ab = 5.39%) and *Rumex obtusifolius* (Ab = 5.32%).

### Effect of environmental covariates on plant diversity, species richness and biomass

#### Correlation tests

Results derived from Pearson's correlation tests (Fig. 4a, b) showed a strong negative correlation between plant dry biomass and SRP ( $r = -0.68$ ; Fig. 4b) and a low correlation with the rest of the evaluated environmental covariates. Plant diversity ( $H'$ ) exhibited a moderate positive correlation with SRP, SOM and TKN (Fig. 4a, b); a moderate negative correlation with the plant dry biomass ( $r = -0.31$ ; Fig. 4a); and no correlation with the topographic attributes (i.e. slope, shade, aspect, curvature). The cumulative species richness showed a low positive correlation ( $r = 0.28$ ; Fig. 4a) with TKN and did not show a clear relationship with the topographic attributes or plant biomass.

#### Regression trees

The fitted regression trees (Fig. 5a–f) show a significant goodness of fit in all cases (Fig. 6a–f; Table 4). The importance of each predictor variable within the regression trees after pruning is shown in Table 4. It is worth noting that the factor variable 'slope stratum' was treated as a surrogate of nitrogen differences across the slope strata for the final interpretation of the regression trees (see "Environmental covariate effect and useful recommendations for slope restoration" section). This approach was adopted to provide a quantitative meaning to the factor slope stratum, and it is supported by the strong strata differences in terms of TKN (Fig. 3d; Wilcke et al. 2003).

**Plant diversity** Slope aspect and hillshade were the main controlling variables of plant diversity ( $H'$ ) when data from both field campaigns were combined (Table 4; Fig. 5a). Aspect (Fig. 2) was the unique predictor (Fig. 5a) for plant diversity when the slope faced southerly (i.e. aspect = 180; Fig. 2) directions. For easterly facing directions (i.e.  $90 < \text{aspect} < 170$ ; Fig. 2), however, other variables were more limiting for plant diversity, in particular TKN (Fig. 5a). Additionally, soil organic matter (SOM) gained relevance when the slope was not fully insulated (i.e. hillshade  $< 255$ ; Fig. 2) (Fig. 5a).

Slope gradient, TKN and curvature were the most important predictor variables for plant diversity when data from the 2015 campaign were used (Table 4; Fig. 5b). TKN was a more relevant predictor when the slope gradient was lower than  $28^\circ$  (Fig. 5b). However, curvature was a better predictor when slope gradient was greater than  $28^\circ$  (Fig. 5b), and the more convex the curvature (i.e. more negative in value; Fig. 2), the more this attribute controlled plant diversity.

**Species richness** TKN and slope stratum were the most relevant predictors for species richness (Table 4; Fig. 5c, d). The fitted trees for species richness clearly identified the crest stratum as a distinct habitat when both years (i.e. 2014 and 2015) were combined (Fig. 5c) and the middle slope stratum with respect to the toe and crest strata when 2015 data were used (Fig. 5d). As for the toe and middle habitats, when the combined set of measurements was used (Fig. 5c), hillshade value hierarchically determined the curvature effect. When shading was greater (i.e. hillshade lower than 255; Fig. 2), a convex curvature (i.e. negative in value; Fig. 2) was more limiting to species richness. Conversely, when insolation was higher (i.e. higher value of hillshade; Fig. 2), a concave curvature (i.e. positive in value; Fig. 2) was shown to affect the species richness.

**Plant biomass** Slope aspect, stratum and soil resistance to penetration (SRP) were the most relevant covariates for plant biomass (Table 4; Fig. 5e, f). As slope orientation became less favourable for irradiation with respect to southerly orientations (i.e. easterly directions;  $90 < \text{aspect} < 170$ ; Fig. 2), the stratum became more important (Fig. 5e) for plant biomass. A lower SRP was directly related to a higher plant biomass (Fig. 5f).

## Discussion

### Signs of landslide-driven slope ecosystem dynamics

Landslide-derived geomorphological processes led to the differentiation of the slope ecosystem into three clearly defined habitats (see "Plant diversity, species richness and slope strata" section; Velázquez and Gómez-Sal 2008; Neto et al. 2017). This differentiation supported the division of the studied slope into three predefined strata (see "Sampling approach" section) and resulted

**Table 2** Plant species indicators for the different studied slope strata or habitats. A species specificity, B species fidelity, IndVal species indicator value, p value statistical significance level, Coverage proportion of sampled quadrats belonging to a given habitat where one or another plant indicator (i.e. species or a species combination) was found. For the middle habitat, the combined coverage is shown

Habitat	Indicator	A	B	IndVal	p value	Coverage (%)
Crest	<i>Galium aparine</i>	0.83	0.65	0.74	0.001	80.00
Middle	<i>Lythrum salicaria</i>	0.76	0.65	0.70	0.001	76.47
	<i>Chamerion angustifolium</i>	1.00	0.18	0.42	0.019	
	<i>Geranium robertianum</i>	1.00	0.18	0.42	0.015	
	<i>Dryopteris pseudodisjuncta</i>	0.99	0.18	0.42	0.038	
Toe	<i>Plantago lanceolata</i>	0.96	0.27	0.51	0.007	59.09

**Table 3** List of plant species found within the study area and their respective botanical families, absolute abundance in the study area (Ab), total biomass (TB), habitat preference (i.e. 1: presence; 0: absence; c: crest; m: middle; t: toe), species indicator value (IndVal), statistical significance as indicator species ( $p$  value) and presence (✓) or absence (X) in the field campaigns carried out (C14: 2014 campaign; C15: 2015 campaign)

Species	Family	Ab (%)	TB (g)	c	m	t	IndVal	$p$ value	C14	C15
<i>Arrhenatherum elatius</i> <sup>a</sup>	Poaceae	5.39	3062.6	1	1	0	0.69	0.04	✓	✓
<i>Rumex obtusifolius</i>	Polygonaceae	5.32	4465.3	1	1	1	0.65	NA	✓	✓
<i>Viburnum acerifolium</i>	Aboxaceae	3.67	2926.5	1	1	0	0.49	0.05	✓	✓
<i>Lythrum salicaria</i> <sup>b</sup>	Lythraceae	3.50	3242.2	0	1	0	0.70	0.001	✓	✓
<i>Onopordum acanthium</i>	Asteraceae	3.44	1904.6	1	1	1	0.66	NA	✓	✓
<i>Silene dioica</i>	Caryophyllaceae	2.98	1704.9	1	1	1	0.74	NA	✓	✓
<i>Daucus carota</i>	Apiaceae	2.86	2215.2	1	1	0	0.50	0.13	✓	✓
<i>Erigeron acris</i>	Asteraceae	2.63	968.0	1	1	1	0.49	NA	✓	✓
<i>Poa pratensis</i> <sup>a</sup>	Poaceae	2.42	605.3	0	1	1	0.64	0.01	✓	✓
<i>Eleocharis lacustris</i>	Cyperaceae	2.35	1294.5	0	1	1	0.42	0.24	✓	✓
<i>Heracleum maximum</i>	Apiaceae	1.67	954.6	1	0	1	0.34	0.41	X	✓
<i>Galium aparine</i> <sup>b</sup>	Rubiaceae	1.64	1170.9	1	0	0	0.73	0.001	✓	✓
<i>Lathyrus pratensis</i>	Fabaceae	1.42	1672.3	1	1	1	0.52	NA	✓	✓
<i>Anthriscus sylvestris</i>	Apiaceae	1.18	627.7	1	1	0	0.40	0.41	✓	✓
<i>Bromus lepidus</i>	Poaceae	0.97	379.3	1	1	1	0.39	NA	✓	✓
<i>Dryopteris pseudodisjuncta</i> <sup>a</sup>	Pteridophyte	0.76	291.8	0	1	0	0.42	0.04	✓	✓
<i>Plantago lanceolata</i> <sup>b</sup>	Plantaginaceae	0.73	103.6	0	0	1	0.51	0.01	✓	✓
<i>Trifolium dubium</i>	Fabaceae	0.71	90.4	0	0	1	0.42	0.34	✓	✓
<i>Phalaris truncata</i>	Poaceae	0.68	62.2	0	1	0	0.24	0.29	✓	✓
<i>Pteridium aquilinum</i>	Dennstaedtiaceae	0.61	171.8	0	0	1	0.21	1.00	X	✓
<i>Convolvulus arvensis</i>	Convolvulaceae	0.55	299.7	1	0	1	0.50	0.17	✓	✓
<i>Cynodon dactylon</i> <sup>a</sup>	Poaceae	0.46	81.0	0	1	1	0.57	0.04	✓	✓
<i>Avena brevis</i>	Poaceae	0.43	327.6	1	1	0	0.37	0.22	✓	✓
<i>Descurainia sophia</i>	Brassicaceae	0.33	248.7	1	1	1	0.32	NA	✓	✓
<i>Sonchus oleraceus</i>	Asteraceae	0.24	194.6	1	0	0	0.22	0.63	X	✓
<i>Urtica dioica</i>	Urticaceae	0.24	162.4	1	1	0	0.46	0.05	✓	✓
<i>Hydrocotyle vulgaris</i>	Apiaceae	0.21	17.0	0	1	1	0.23	0.75	X	✓
<i>Aurina saxatilis</i>	Brassicaceae	0.20	108.4	1	1	1	0.34	NA	X	✓
<i>Trifolium repens</i>	Fabaceae	0.20	35.4	0	0	1	0.37	0.14	✓	✓
<i>Poa annua</i>	Poaceae	0.12	41.7	0	1	1	0.36	0.24	✓	✓
<i>Agrimonia eupatoria</i>	Rosaceae	0.11	36.2	1	0	0	0.38	0.06	✓	X



Table 3 (continued)										
Species	Family	Ab (%)	TB (g)	c	m	t	IndVal	p value	C14	C15
<i>Vicia cracca</i>	Fabaceae	0.11	23.0	0	0	1	0.37	0.09	✓	✓
<i>Lolium perenne</i>	Poaceae	0.09	16.4	0	0	1	0.21	1.00	✓	✓
<i>Crepis biennis</i>	Asteraceae	0.07	27.8	1	0	1	0.26	0.94	X	✓
<i>Chamerion angustifolium</i> <sup>a</sup>	Onagraceae	0.06	41.3	0	1	0	0.42	0.02	✓	✓
<i>Bromus mollis</i>	Poaceae	0.05	14.6	0	0	1	0.21	1.00	✓	✓
Orchid	Orchideaceae	0.03	4.8	0	0	1	0.21	1.00	X	✓
<i>Geranium robertianum</i> <sup>a</sup>	Geraniaceae	0.02	13.7	0	1	0	0.42	0.01	X	✓
<i>Vicia bithynica</i>	Fabaceae	0.02	20.1	0	0	1	0.21	1.00	✓	✓
<i>Papaver rhoeas</i>	Papaveraceae	0.01	4.8	1	0	0	0.22	0.63	X	✓
<i>Salvia pratensis</i>	Lamiaceae	0.002	2.8	0	1	0	0.24	0.29	✓	X
<i>Erodium cicutarium</i>	Geraniaceae	0.001	1.5	0	0	1	0.21	1.00	✓	X

p value = NA: plant species occur in all sites and cannot be statistically tested

<sup>a</sup> Significant at 95% confidence level; plant species indicator on the basis of the statistical significance of IndVal

<sup>b</sup> Significant at 99% confidence level

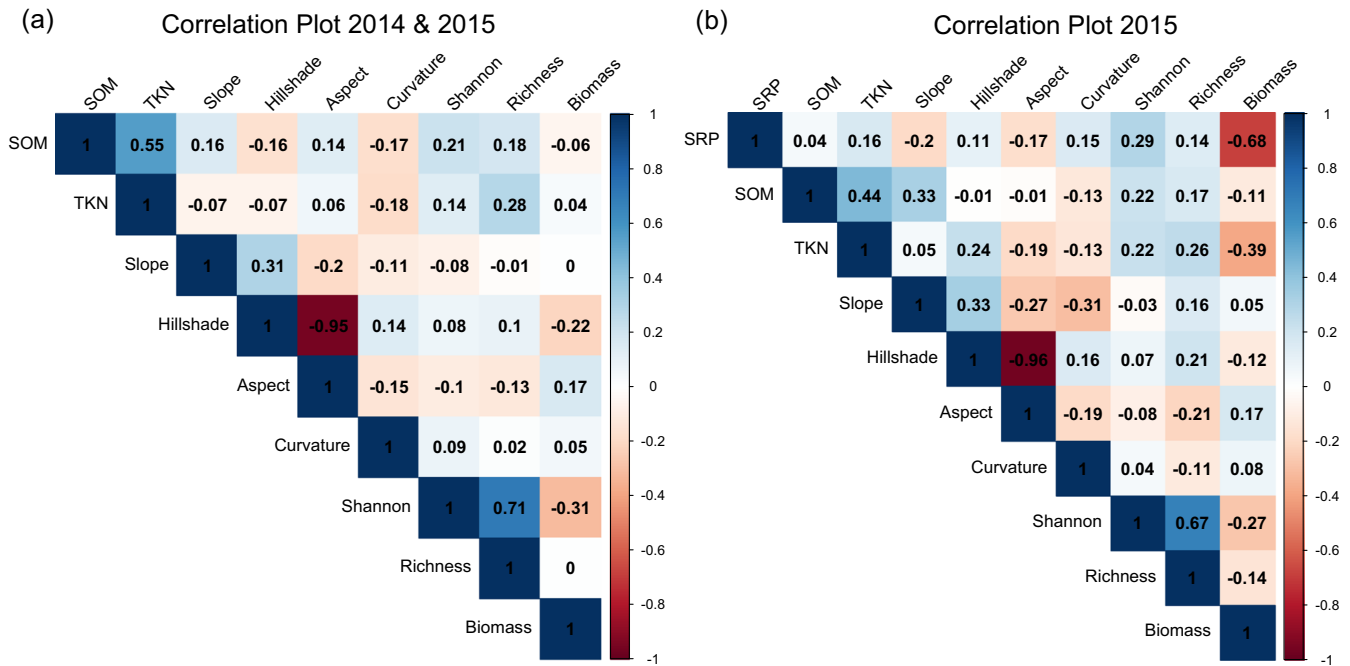
from an increase in biophysical diversity (Geertsema and Pojar 2007).

The increase in biophysical diversity was evident in terms of the encountered differences in SRP (Fig. 3c). The toe habitat showed a much higher SRP than the crest (Fig. 3c). This outcome may be related to landslide-driven changes in the local soil texture, porosity and density (Geertsema and Pojar 2007) which, in turn, are linked to the geotechnical properties of the slope-forming materials (see “Study site” section) exposed after the shallow landslide episodes. Settlement and consolidation processes fostered by wetting and drying meteorological cycles after the landslide events could have increased the soil density at the toe (Craig 2004; Head and Epps 2011). The plastic nature of the bare soil, related to the soil fine fraction (see “Study site” section), may have contributed to an increase in soil firmness at the middle stratum following wetting and drying cycles (Consentini and Foti 2014). As a result, SRP increased in the exposed strata subject to slope failure (i.e. middle and toe). Alternatively, SRP differences (Fig. 3c) could be due to other landscape evolution processes triggered by landslides (see in the following; Walker et al. 2009).

The differences in species richness between the slope strata (Table 1; Fig. 3b) could be interpreted as a sign of landscape evolution (Dale et al. 2005; Velázquez and Gómez-Sal 2008). For example, species richness was lower at the crest, which has been stable for a longer period than the other two studied slope zones (Fig. 3b). The disturbance-free periods could have facilitated the establishment and succession of plant communities (del Moral and Jones 2002). Once plant communities were established, competitive exclusion may have arisen (Wilson and Tilman 1995), decreasing species richness (Herbert et al. 2004). The absence of disturbance would have facilitated the formation of slope soil (Myer and Walker 1997; Smale et al. 1997), fostered by the incorporation of plant-derived decaying organic matter (Fig. 3e), thus improving the soil structure (Bronick and Lal 2005) and reducing the SRP (Fig. 3c; Franzluebbers 2002). Nonetheless, we believe that the temporal expansion of this study could contribute towards the elucidation on whether our observations can be interpreted as signs of hillslope evolution.

Conversely, landslide recurrence may have led to an increase in species richness (Velázquez and Gómez-Sal 2009) in the middle and toe strata (Table 1; Fig. 3b; Neto et al. 2017). Lower levels of plant competition found in the nutrient-rich gaps produced by shallow landslides support this observation (Walker et al. 1996). In particular, the lack of herbaceous plant competition for light with higher-order plants (e.g. woody species) could be the reason for the higher comparative species richness found after disturbance in landslide-prone zones (e.g. Myer and Walker 1997; Rajaniemi et al. 2003; Soto et al. 2017).

The active role of shallow landslides on slope ecosystem differentiation was also shown by the accumulation of nitrogen at the lowest slope stratum (i.e. toe; Fig. 3d; Wilcke et al. 2003). It is highly likely that this was a result of the downward movement of nutrient-rich soil volumes following slope failure, albeit nitrogen leaching from the crest soil after rains could be possible as well (e.g. Hood et al. 2003). Based on this result, nitrogen could be the key abiotic factor that facilitated the establishment of vegetation within the gaps opened up by landslides (Walker and del Moral 2003; Shiels et al. 2008) and one of the main factors triggering further ecosystem dynamics (e.g. Herbert et al. 2004). The higher



**Fig. 4** Correlation (i.e. Pearson's correlation coefficient) between the three considered plant diversity metrics (i.e. Shannon index, species richness and aboveground plant dry biomass) and the considered environmental covariates for **a** the combination of 2014–2015 field campaigns and **b** the 2015 field campaign. *SRP* soil resistance to penetration, *SOM* soil organic matter, *TKN* soil total Kjeldahl nitrogen, *Slope* slope gradient, *Hillshade* topographic hillshade, *Aspect* topographic azimuth, *Curvature* topographic surface curvature. The darker the shade the higher the correlation. Blue colour: positive correlation; red colour: negative correlation

nitrogen levels observed in the two lower slope strata in 2014 (Fig. 3d) could explain the higher plant biomass observed there (Fig. 3f; Gross and Collins 2000; Herbert et al. 2004) if adequate nitrogen mineralisation is assumed (Urbano 1995). TKN differences between the two sampling campaigns (Fig. 3d), supported by correlated plant biomass differences (Fig. 3f), may reflect consumption of nitrogen by the plant community established on the slope after disturbance: the higher levels of soil nitrogen allowed more plant biomass development during 2014 (Dalling and Tanner 1995; Rowe et al. 2006). As a result, the levels of soil nitrogen decreased in the subsequent season (Fig. 3d; Niklaus et al. 2001) and led to lower biomass production (Fig. 3f). Nonetheless, soil nitrogen could have also led to an increase in belowground plant competition and, consequently, in reduction of plant aboveground biomass (Rajaniemi et al. 2003; Herbert et al. 2004), as seen in the results from 2015 (Fig. 3d, f) and supported by the correlation tests (Fig. 4a). These processes may have led to a decrease in plant diversity (Gross and Collins 2000; Rajaniemi et al. 2003), hinted at in the results from the toe stratum in 2015 when compared to 2014 (Fig. 3a, b).

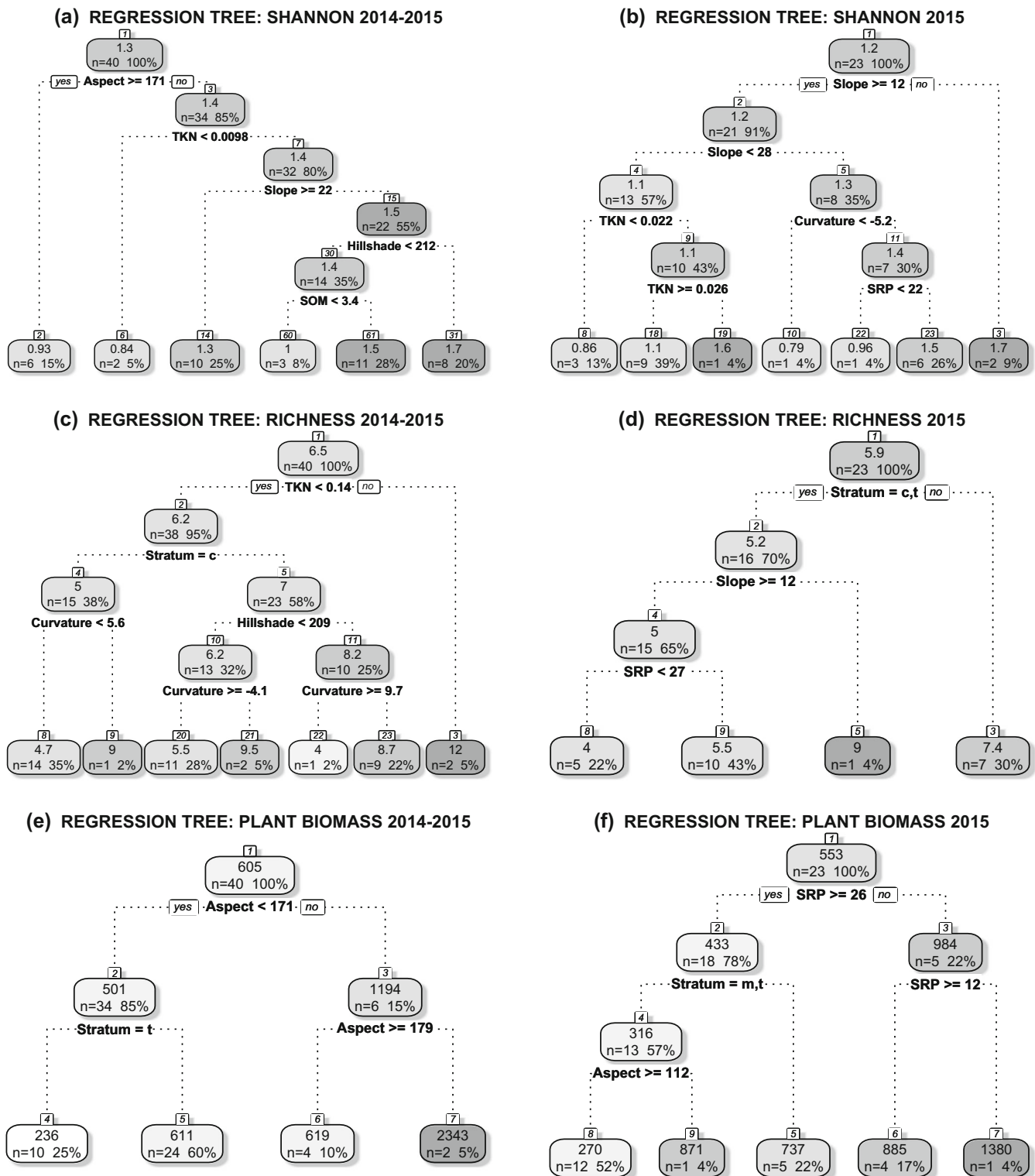
#### Plant diversity metrics as signs of slope ecosystem self-organisation

Species richness differences between the slope strata (see “Plant diversity, species richness and slope strata” section; Fig. 3b) may result from the self-regulating capacity of the slope ecosystem after disturbance (Neto et al. 2017). The downward movement of nutrient-rich materials and the way that plant communities respond (e.g. through competing for light and nutrients) played a key role in the self-organisation process (Walker et al. 1996), as discussed earlier (see 4.1). As a result, species richness showed

evident differences between the slope strata (Table 1; Fig. 3b). These were consistent with the findings of other authors (e.g. Armesto and Pickett 1985; Myster and Walker 1997; Walker et al. 2006; Elias and Dias 2009; Velázquez and Gómez-Sal 2009; Neto et al. 2017) and with the intermediate disturbance hypothesis (Connell 1978).

In terms of species composition, the Bray-Curtis similarity index (see “Plant diversity, species richness and slope strata” section) highlighted a distinct toe habitat during both sampling campaigns and showed clear differences between 2014 and 2015 (see “Plant diversity, species richness and slope strata” section). This may suggest an increasing system complexity as the landscape starts recovering from disturbance (Odum 1969; Myster and Walker 1997; Velázquez and Gómez-Sal 2009). The relatively high species evenness ( $J'$ ) encountered (Table 1) indicates an absence of dominant species and, thus, may suggest an early successional stage within the plant community of our study site (Mulder et al. 2004).

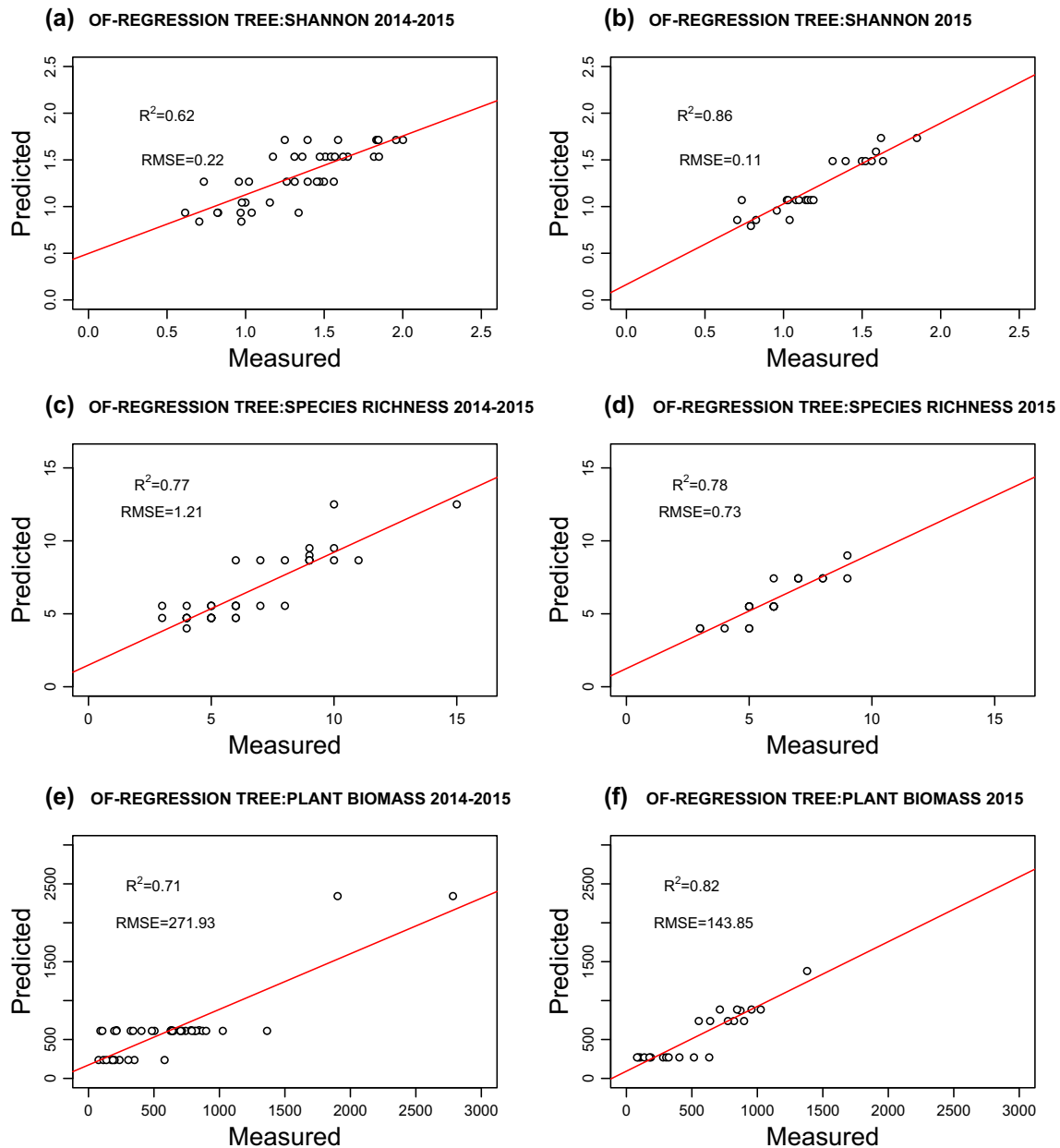
The plant diversity ( $H'$ ) on the study site (Table 1; Fig. 3a) was below or within the range reported by other diversity studies focusing on grasslands (e.g. Bochet and Garcia-Fayos 2004; Kahmen et al. 2005; Spehn et al. 2005; Pohl et al. 2009). Although plant diversity ( $H'$ ) did not differ between slope strata (Table 1; Fig. 3a), the observed  $H'$  values with respect to the ones provided in the literature could suggest an adequate plant colonisation and establishment on the studied slope. Many plant species found (Table 3) were common weeds (BRC 2016), usually present on disturbed grounds, indicating that most of them entered the community from the adjacent landscape (Velázquez and Gómez-Sal 2008). Overall, the species



**Fig. 5** Regression tree dendrograms for the different fitted models. **a** Shannon diversity for the 2014 and 2015 campaigns. **b** Shannon diversity for the 2015 campaign and including SRP. **c** Species richness for the 2014 and 2015 campaigns. **d** Species richness for the 2015 campaign including SRP. **e** Aboveground plant dry biomass for the 2014 and 2015 campaigns. **f** Aboveground plant dry biomass for the 2015 campaign including SRP. Each tree leaf (i.e. box) indicates the mean response, number and percentage of observations. Interpretation of the topographic attribute (i.e. aspect, hillshade, curvature) values is shown in Fig. 3

assemblage was relatively similar between the studied slope strata (Table 3) indicating that many species could have been

dormant in the displaced soil materials as seeds or propagules (e.g. Myster and Walker 1997).



**Fig. 6** Objective functions (OF) for the different fitted regression trees. **a** Shannon diversity for the 2014 and 2015 campaigns excluding SRP. **b** Shannon diversity for the 2015 campaign including SRP. **c** Species richness for the 2014 and 2015 campaigns excluding SRP. **d** Species richness for the 2015 campaign including SRP. **e** Aboveground plant dry biomass for the 2014 and 2015 campaigns excluding SRP. **f** Aboveground plant dry biomass for the 2015 campaign including SRP. SRP soil resistance to penetration

Relating these observations to the self-regulation of a slope after disturbance, some ideas can be drawn regarding the early stages of human-driven restoration actions on slopes, which usually include planting a single or few plant species. More than 40 plant species were identified in the initial stages of slope colonisation in this study (Table 3), suggesting that planting with a higher species diversity would be more ecologically relevant. In some instances, landslide-derived gaps can be overwhelmed by alien species that make the most of the low levels of plant competition in these patches to the detriment of native species (Catford et al. 2012). In this regard, two alien species were found within the

studied slope with a relative high abundance (Table 3): *Heracleum maximum* and *Viburnum acerifolium*. This highlights an important issue to consider when planning planting strategies.

#### Plant species as indicators of landslide-driven biophysical diversity

Plant indicator species results (Table 2) corroborated the differentiation of the slope into distinct habitats and provided further support to the notion that landslides may increase biophysical diversity. For instance, the principal indicator for the middle slope habitat, *Lythrum salicaria*, is a herbaceous species belonging to wet habitats and slow-flowing creeks (BRC 2016). As the slope failed, the phreatic



**Table 4** Regression tree outcomes showing the coefficient of determination ( $R^2$ ), residual mean square error (RMSE) and variable importance expressed in %

Response variable	Model	$R^2$	RMSE	Slope gradient	Aspect	Hillshade	Surface curvature	TKN	SOM	SRP	Stratum
Plant diversity	A	0.62	0.22	10	24	26	4	13	23	–	0
	B	0.86	0.11	36	4	4	15	16	12	10	3
Species richness	A	0.77	1.21	3	9	10	26	34	6	–	13
	B	0.78	0.73	34	5	7	5	2	0	11	35
Plant biomass	A	0.71	271.93	19	29	18	0	20	9	–	5
	B	0.82	143.85	0	16	0	13	10	0	42	18

Model A includes information from 2014 and 2015 field campaigns without the soil resistance to penetration; model includes soil resistance to penetration as a predictor variable and information from the 2015 field campaign only  
TKN soil total Kjeldahl nitrogen, SOM soil organic matter, SRP soil resistance to penetration, Stratum factor variable including the three considered slope strata in the study (i.e. crest, middle and toe)

zone was exposed in some areas within the slope's middle zone, creating an entire foreign aquatic habitat that did not exist before within our slope ecosystem. Likewise, the indicator for the crest habitat, *Galium aparine*, might have thrived as a consequence of small mammals, such as rabbits, dispersing its seeds over the crest habitat (BRC 2016). Despite the former speculation, the crest of the slope remained stable during the last slope failure episode (see "Study site" section), allowing the prolonged stability to host mammals (i.e. rabbits, cats and mice), as noticed by the authors during the sampling campaigns. Moreover, the plant indicator species identified for the toe habitat, *Plantago lanceolata*, may suggest modifications to the slope geochemistry, as many of the species identified within the slope (Table 3) are generally associated with calcareous or basic (i.e. pH >7) soils (BRC 2016), while *Plantago lanceolata* generally thrives on more acidic soils (i.e. pH <7). The outcomes derived from the plant indicator analysis (Tables 2 and 3), however, should be taken with caution as the fidelity (i.e. B; Table 2) for most of the identified indicators was low, and the coverage (Table 2) did not reach 100%. Nonetheless, the use of the plant indicator species analysis (Dufrene and Legendre 1997; De Caceres and Legendre 2009) presented here opens up an exciting possibility to explore landslide-derived habitats and establish different slope restoration and management strategies in accordance with the features of a given slope habitat.

#### Environmental covariate effect and useful recommendations for slope restoration

Our results are consistent with the hypothesis that slope topography has a significant effect on establishment and dynamics of vegetation (e.g. Bochet and Garcia-Fayos 2004; Gallardo-Cruz et al. 2009; Moeslund et al. 2013; Stein et al. 2014) after landslides. Terrain attributes such as slope gradient, aspect, hillshade and curvature (Fig. 2) play a vital role in the establishment of vegetation as they are intimately related to the availability of natural resources (e.g. nutrients, light, water) to plants (e.g. Fu et al. 2004; Gallardo-Cruz et al. 2009; Yu et al. 2015). These effects were seen after fitting regression tree models (Table 4; Figs. 5a–f and 6a–f), which showed hierarchies of importance among topographical attributes and with their associated environmental covariates, such as light and nitrogen (see "Regression trees" section). The effect of the evaluated environmental covariates varied depending on the vegetation metric to be predicted (Table 4), the direction of change of one factor in response to the level of another factor and the amount of information employed to fit the regression tree (i.e. 2014–2015: Fig. 5a, c, e; 2015: Fig. 5b, d, e). It is worth noting that the factor variable slope stratum was treated as a surrogate of nitrogen differences across the slope strata for the final interpretation of the regression trees, as indicated in "Regression trees" section. Overall, five main aspects related to post-landslip establishment of plant communities on slopes were confirmed with the regression trees:

1. Soil nitrogen and light availability have a strong effect on plant diversity ( $H'$ ; Fig. 5a, b), species richness (Fig. 5c, d) and plant biomass (Fig. 5e, f) as noted previously in the literature (e.g. Myster and Walker 1997; Rajaniemi et al. 2003; Herbert et al. 2004; Pykälä et al. 2005; Shiels et al. 2008; Gallardo-Cruz et al. 2009; Soto et al. 2017).
2. The amount of incoming light with respect to the level of soil nitrogen can regulate plant diversity (Fig. 5a, c) and biomass (Fig. 5e). Thus, trade-offs may occur between light and

- nitrogen (Fig. 5a, c, e; e.g. Walters and Reich 1997; Rajaniemi et al. 2003; Herbert et al. 2004; Soto et al. 2017) and their effect upon plant communities must be evaluated together.
3. Slope topography governs the availability of both nitrogen (Weintraub et al. 2015) and light (Gallardo-Cruz et al. 2009) (Fig. 5a, b, e, f). The spatial availability of nitrogen can be limited by the topographical exposure (i.e. slope gradient and curvature; Chapman 2000), where a higher slope gradient and a more convex curvature (i.e. negative in value; Fig. 2) will constrain the formation of soil and the accumulation of nutrients (Fig. 5b; Heimsath et al. 1997; Bertoldi et al. 2006; Weintraub et al. 2015). On a landslide-prone slope, however, landslide dynamics will exert a greater control over the availability of nitrogen (e.g. Guariguata 1990; Walker et al. 1996; Myster and Walker 1997; Velázquez and Gómez-Sal 2008) than the topographical exposure, supported here by the differentiation of the studied slope into habitats (Figs. 3d and 5c, e, f; Walker et al. 1996; Velázquez and Gómez-Sal 2008; Neto et al. 2017). With regard to light availability, we used the hillshade parameter in our approach, knowing that it is intended as a cartographical representation option to enhance the graphical representation of the study site topography (e.g. Zu 2016) and, therefore, carried little ecological meaning. Although its use provided relevant results, for the future, it would be advisable to employ indices aiming at estimating solar radiation input in order to better clarify the effect of light on plant communities (e.g. topographic radiation index; Piedallu and Gegout 2008).
  4. Topographical exposure may also control plant diversity (i.e.  $H'$  and richness; Table 1; Fig. 5b, d). High slope gradients and convexity (Fig. 2) may have a negative impact on plant establishment (Bochet and Garcia-Fayos 2004). As a result, it is likely that plant communities will develop less in zones of high topographical exposure (i.e. more prone to shallow landslides; Lu and Godt 2013), where the diversity of early successional species will be maintained at relatively high levels (Velázquez and Gómez-Sal 2008) compared to more stable zones undergoing plant succession (e.g. crest of the studied slope and undisturbed sections of the slope).
  5. The SRP is a viable and readily measurable indicator of slope habitat (Fig. 3c) and plant biomass (Fig. 5f). Soil penetrability is related to soil structure (Franzluibbers 2002): a lower SRP (i.e. higher penetrability) will be indicative of better soil physical conditions for plant establishment (Bengough and Mullins 1990) and, therefore, for more plant biomass development. It is worth noting that plant biomass development is of high interest in terms of slope stabilisation with plants (e.g. Gonzalez-Ollauri and Mickovski 2016).

Overall, the earlier outcomes indicate that regression trees are a viable tool for evaluating and understanding the hierarchical complexity of slope ecosystems, which may not be fully detected with Pearson's correlation test (Fig. 4a, b). The information obtained from the regression trees (Fig. 5a–f) can be directly applied in the implementation of slope restoration strategies against shallow landslides involving the use of vegetation (e.g. Norris et al. 2008; Mickovski 2014; Tardio and González-Ollauri 2016). For example, a balanced application of soil amendments (e.g. nitrogen and OM-rich compost) on shaded zones of the slope could foster the

establishment of a dense and more diverse early-stage plant community (e.g. Walters and Reich 1997; Elmarsdottir et al. 2003; Rowe et al. 2006) or root systems (Mickovski and Ennos 2003; Gonzalez-Ollauri and Mickovski 2016). Care must be taken on slope zones presenting high topographical exposure to obtain adequate vegetation establishment. On these zones, human-driven revegetation strategies, such as facilitation (e.g. Brooker et al. 2008), could be implemented. Information related to SRP could be used to implement soil tillage on certain slope zones to improve the physical properties of soil (Bronick and Lal 2005), which, combined with the application of soil amendments, can facilitate the establishment of a dense plant cover (e.g. Bengough and Mullins 1990; Wilson and Tilman 1995) on the slope.

## Conclusions

In the light of our results and observations, we can conclude that

- Shallow landslides are dynamic geomorphological processes contributing to biophysical diversity and able to distinguish the landscape into different slope habitats even at small spatial scales.
- The slope habitats can be distinct in terms of plant species richness and compositional differences, as well as in terms of soil properties such as nitrogen content and resistance to penetration.
- Differences in plant species richness throughout the slope habitats are a direct consequence of the slope ecosystem self-regulating capacity after disturbance.
- Soil nitrogen and light availability have a strong effect on plant establishment (i.e. plant diversity, richness and biomass) after disturbance.
- Landscape topography and landslide dynamics play an important role on soil nitrogen and light availability and, hence, on landscape evolution and its self-regulating capacity.
- Certain plant species may be good indicators of landslide-driven biophysical diversity.
- The effects of the environmental covariates on plant diversity metrics can be effectively appraised with regression tree models.

A comprehensive novel approach has been presented here to detect traits of ecosystem evolution, self-regulation and biophysical diversity triggered by shallow landslides. We acknowledge that the results presented herein refer to a particular site with specific environmental conditions and to a limited monitoring time. Further research along the lines presented in this study and, over longer periods of time, larger spatial scales is needed to shed more light on how shallow landslide-prone ecosystems evolve after slope disturbance. Undoubtedly, the approach presented herein provides a good basis to explore shallow landslides within an ecological perspective and to apply the resulting knowledge into the sustainable restoration of landslide-prone slopes.

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