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REGULAR ARTICLE

Telling a different story: plant recolonization after landslides under a semi-arid climate

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Abstract
Aims We aimed to know how plant species colonize landslides under a semi-arid climate.
Methods We selected 30 landslides triggered by the continuous rainstorms in the hilly-gullied region of the Chinese Loess Plateau in July 2013. We quantified post-landslide changes in a core list of soil properties, vegetation properties and plant functional traits and also analyzed their relationships.
Results After landslides, there were no large changes in the soil properties except slope angle. Correspondingly, there were no large changes in plant species richness, species composition and the functional traits. The vegetation cover of scars (the newly exposed soil surfaces because of landslides) was significantly lower than those of deposits (the deposition zones of landslides) and undisturbed vegetated areas surrounding the landslides (control areas), but the vegetation recovery of scars should be only a matter of time.
Conclusions Under the semi-arid climate of the area, landslides do not have profound effects on soil properties and plant species richness and composition, telling a different story from those landslides under other climate regimes and implying great potential for the restoration of landslides.

Keywords Semi-arid climate · Landslide · Plant recolonization · Plant-soil interaction · Plant functional trait · Ecological restoration

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Introduction

Landslides are natural geomorphologic processes that continuously shape landscapes in most mountainous regions of the world (Xu et al. 2007; Restrepo et al. 2009; Sidle and Bogaarda 2016; Arnáez et al. 2017). They are also a severe form of natural disturbance that can deplete the productivity of slope ecosystems in a very short time, and they require a quite long time for restoration (Guariguata 1990; Dalling 1994; Restrepo et al. 2003). The down-slope removal of soil and vegetation caused by landslides has aroused an increasing number of explorations into plant recolonization and ecological restoration theories (Lundgren 1978; Guariguata 1990; Walker et al. 1996; Velázquez and Gómez-Sal 2007; Restrepo et al. 2009; Walker et al. 2009; Walker and Shiels 2013; Neto et al. 2017).

Plant species composition (represented by species occurrence or species abundance) on landslides is usually different from that on the surrounding undisturbed substrates (Guariguata 1990; Restrepo and Vitousek 2001; Velázquez and Gómez-Sal 2007; Neto et al. 2017). In addition to increased light into treefall gaps in montane forests (Guariguata 1990; Myster and Femández 1995), these post-landslide vegetation changes can be associated with large changes in soil properties caused by landslides (Restrepo and Vitousek 2001; Lozano and Bussmann 2005). After landslides, the original slopes become steeper, and the soils turn arid and infertile (Lundgren 1978; Dalling and Tanner 1995; Wilcke et al. 2003). Steep slopes can present difficulties for seed fixation and plant persistence on hillslopes (Cerdà and García-Fayos 1997; Bochet et al. 2009). A substantial decrease in the availability of soil moisture can inhibit seed germination and reduce seedling survival (García-Fayos et al. 2000; Bulmer and Simpson 2005). Likewise, a substantial decrease in soil fertility can reduce seedling survival and growth (Record et al. 2016). Therefore, the new soil surfaces produced by landslides may act as a filter in the process of plant recolonization, thus filtering out the species whose traits reflect lower fitness for the new soil conditions and also restricting the relative abundance of colonizing species. Or in other cases, the new soil surfaces may be favorable to the successful colonization of the surrounding rare or minor species, such as *Orchis italica* and *Anacamptis pyramidalis* on Mediterranean landslides (Neto et al. 2017), thus they may also act as a temporary shelter, or a diversity reservoir. In addition, the new soil surfaces may be susceptible to the invasion of exotic species, thus unfortunately becoming an invaded system, such as the landslides in the Ninole ridges on the island of Hawai'i and the large landslide on the Casita Volcano of Nicaragua (Restrepo and Vitousek 2001; Velázquez and Gómez-Sal 2007).

Within landslides, scars (the newly exposed soil surfaces) are typically characterized by persistent erosion, infertility and propagule unavailability, while deposits (the down-slope deposition zones of landslides) are relatively stable and commonly considered as a rich mixture of displaced soil and plants (Guariguata 1990; Myster and Femández 1995; Velázquez and Gómez-Sal 2008; Walker and Shiels 2008). Plant species composition on scars has been found to be different from that on deposits (Guariguata 1990; Velázquez and Gómez-Sal 2007), probably because the differences between scars and deposits in stability, fertility and the availability of propagules drive two different ways for plant species to colonize. For example, within a landslide on the Casita Volcano of Nicaragua, *Trema micrantha* (L.) Blume exhibits different growth strategies on scars and deposits, being short and thin on scars but highly variable in stem height and diameter on deposits (Velázquez and Gómez-Sal 2009); moreover, a 'small'-seed morphotype (represented by seeds of *Trema micrantha* (L.) Blume) and a 'large'-seed morphotype (represented by seeds of *Muntingia calabura* L.) are fit for the unstable and infertile condition of scars and the stable and comparatively fertile condition of deposits, respectively (Silvera et al. 2003; Velázquez and Gómez-Sal 2007). In addition, long-distance seed dispersal and vegetative expansion from adjacent plants are critical for scars, while in situ germination of displaced seeds, resprouting of plant remnants and survival of displaced plants should be more common for deposits (Lundgren 1978; Guariguata 1990; Restrepo et al. 2009). Likewise, the plant species whose seeds are more capable of resisting erosion forces and germinating quickly should be dominant on scars by reference to previous research on eroded slopes under semi-arid climates (Bochet et al. 2007; Wang et al. 2011a; García-Fayos et al. 2013). The trait-based approach may provide unique mechanistic insights into plant-soil interactions in the process of plant recolonization after landslides, but it has not been extensively applied in this field.

Plant recolonization after landslides has been well studied in tropical or temperate montane forests characterized by humid environments and light competition between plants (Walker et al. 1996; Restrepo et al. 2009; Walker and Shiels 2013), but there is still little information concerning plant recolonization after landslides somewhere under other climate regimes, such as a semi-arid climate. Under semi-arid climates, the critical issue for plant colonization is to overcome drought as well as soil erosion (Bochet et al. 2007, 2009; Wang et al. 2011a; Bochet 2015). The hilly-gullied region of the Chinese Loess Plateau suffers from a long history of drought and soil erosion due to the climatic, geomorphologic and edaphic characteristics, as well as intense human activities for millennia (Li et al. 2008). Landslides are common and catastrophic events in this region (Liu and Wu 1996; Li et al. 2008), and they left a deep imprint on the region because of the continuous rainstorms in July 2013 (Cao et al. 2015), thus providing us with a good opportunity to study plant recolonization after landslides under a semi-arid climate.

The objective of this study was to know how plant species colonize the new soil surfaces produced by landslides under a semi-arid climate. Based on the previous knowledge, we hypothesized that under this climate regime, landslides would also exert profound effects on soil properties and then on vegetation properties involving vegetation cover, species richness and species composition. We also hypothesized that plant-soil interactions during plant recolonization could be revealed through post-landslide change in plant functional traits related to dispersal, establishment and persistence. To test it, we selected 30 landslides triggered by the continuous rainstorms in the hilly-gullied region of the Chinese Loess Plateau in July 2013. Then, we quantified post-landslide changes in soil properties, vegetation properties and plant functional traits and also analyzed their relationships. Finally, we discussed the process of plant recolonization after landslides and the restoration potential of landslides in the area.

Materials and methods

Study area

This study was conducted in the Majiagou (36°49′–36°56′ N, 109°09′–109°18′ E), Yaozigou (36°47′–36°49′ N, 109°15′–109°20′ E), Fangta (36°47′–36°49′ N, 109°14′–109°16′ E) and Xiannangou (36°41′–36°44′ N, 109°13′–109°18′ E) watersheds (Ansai County, Shaanxi Province, China), at altitudes between 1100 and 1450 m a.s.l. in the hilly-gullied region of the Chinese Loess Plateau.

Climate is cold and semi-arid (BSk; Köppen 1884). Average annual temperature is around 9 °C, and annual precipitation is around 500 mm (50–70% occurring from July to September and mostly in the form of rainstorms) (Li et al. 2008).

Soils are mainly silty-loam, with pH values of 7.6–8.5, soluble salts less than 1 g kg^{-1} and internal friction angles around 25° (Guo et al. 1992; Liu and Wu 1996). Moreover, the area of slopes with slope angles >25° (that are prone to failure) comprises 33.9 ± 3.4% of the watershed area in 2014 (Chen, unpublished data).

Vegetation covers 61.1 ± 8.9% of the watershed area in 2014 (Chen, unpublished data). The natural vegetation is characteristic of a transition between forests and steppe, and it is dominated by subshrubs (*Artemisia gmelinii* Web. ex Stechm., *Artemisia giraldii* Pamp. and *Lespedeza daurica* (Laxm.) Schindl. var. *daurica*) and herbs (*Stipa bungeana* Trin., *Poa sphondylodes* Trin., *Cleistogenes caespitosa* Keng, *Leymus secalinus* (Georgi) Tzvel., *Bothriochloa ischaemum* (L.) Keng, *Heteropappus altaicus* (Willd.) Novopokr., *Patrinia heterophylla* Bunge and *Artemisia scoparia* Waldst. et Kit.) (Li et al. 2008). Shrubs are typically sparse, including *Periploca sepium* Bunge, *Sophora davidii* (Franch.) Skeels var. *davidii*, *Buddleja alternifolia* Maxim. and *Syringa oblata* Lindl. var. *oblata*, among others (Li et al. 2008). The area has a long history of cultivation, grazing and exploitation that disturbed the natural vegetation and caused serious soil loss, but several native plants and exotic plants (e.g., *Robinia pseudoacacia* L. var. *pseudoacacia*, *Salix matsudana* Koidz. var. *matsudana*, *Populus simonii* Carr. var. *simonii*, *Hippophae rhamnoides* L. and *Caragana korshinskii* Kom. f. *korshinskii*) have been extensively used for large-scale restoration programs since 1999 (Li et al. 2008). There are also economic forests in the area, dominated by *Malus pumila* Mill. and *Cerasus pseudocerasus* (Lindl.) G. Don.

The geomorphologic, climatic and edaphic characteristics as well as the intense human activities make the area very prone to landslides (Liu and Wu 1996; Li et al. 2008). In addition, landslides occurring in the area are mostly shallow-seated types (<2 m deep; Sidle and Ochiai 2006), which occur often in a large quantity and should be the main source of soil erosion in the area (Zhang and Li 2011).

Sampling design

In July 2014, 30 landslides were carefully selected out of hundreds of landslides caused by the continuous rainstorms in the area in July 2013 (Table 1). These selected landslides occurred at different elevations and aspects and were shallow-seated, and there were no signs of recent landslides in the surrounding vegetated areas. The location, elevation and aspect of each landslide were measured using a hand-held GPS (UG903S;

Table 1 Topographic information of the 30 landslides

Landslide number	Elevation (m a.s.l.)	Aspect (°)	Erosion depth (cm)
1	1275	95	29.7 ± 1.5
2	1252	320	30.0 ± 1.0
3	1209	80	20.3 ± 4.5
4	1202	80	30.0 ± 1.3
5	1253	150	38.8 ± 8.5
6	1249	140	21.7 ± 2.9
7	1246	348	30.3 ± 3.2
8	1264	140	19.7 ± 2.5
9	1265	200	33.8 ± 4.8
10	1238	140	19.8 ± 1.8
11	1239	140	27.3 ± 2.5
12	1265	125	30.3 ± 0.6
13	1243	5	29.8 ± 1.7
14	1260	165	20.3 ± 5.6
15	1271	338	20.0 ± 2.6
16	1121	20	31.3 ± 9.5
17	1147	335	29.7 ± 4.0
18	1247	348	30.8 ± 4.3
19	1249	340	35.3 ± 4.5
20	1236	85	20.0 ± 2.8
21	1274	140	20.0 ± 1.6
22	1273	140	19.7 ± 3.5
23	1273	140	49.3 ± 4.0
24	1276	220	33.3 ± 5.8
25	1274	185	22.5 ± 8.4
26	1244	40	19.8 ± 1.3
27	1187	295	19.5 ± 1.7
28	1190	295	20.5 ± 2.5
29	1188	315	20.3 ± 2.3
30	1189	300	21.0 ± 1.7

Beijing Unistrong Science and Technology Co., Ltd., Beijing, China). Erosion depth, the average depth of soil removal by a landslide, was measured in at least three points of each landslide using a straightedge. The measuring points for each landslide were evenly distributed along the landslide edge.

For each landslide, we investigated two zones within the landslide: the scar (the newly exposed soil surfaces) and the deposit (the down-slope deposition zone of the landslide); we also investigated the undisturbed vegetated area surrounding the landslide (within 20 m from the landslide edge), which has been commonly considered as the vegetation state reference and the main propagule source for landslides (Lundgren 1978; Walker et al. 1996) and thus was used as a control area.

We determined the geographical coordinates of each of the two landslide zones and the surrounding vegetated areas using the GPS, and then we calculated geographical distances among all these sites using ArcGIS (version 10.2, Environmental Systems Research Institute, Inc., Redlands, California, US). We also measured the slope angle of each of the two landslide zones and the surrounding vegetated areas using a slope scale (JZC-B2; Bofei Construction Instruments Co., Ltd., Suzhou, China) with three repetitions.

Vegetation properties

A vegetation survey was conducted in mid-July 2015 (the peak of the growing season in the area). For each landslide, we estimated vegetation cover, identified all plant species and recorded the number of individuals of each plant species on the entire surface of the scar, the entire surface of the deposit, and each of six quadrats (2×2 m) evenly distributed in the surrounding vegetated area. Vegetation cover was estimated visually by three observers. The number of plant species that appeared in each of the two landslide zones and the surrounding vegetated areas was used as an estimate of species richness. The number of individuals of each clonal species that appeared was recorded by counting the number of its patches (all the stems in a patch were considered as parts of one individual). Species density, known as the most relevant measure of demographic processes (Lepš et al. 2006), was considered as an appropriate estimate of species abundance in each of the two landslide zones and the surrounding vegetated areas. To estimate the density of each plant species in each landslide zone, we determined the areas of the scar and the deposit of each landslide (Table S1) by taking vertical photographs in the field with a scale reference and then analyzing them with the Image-Pro PLUS software (version 6.0; Media Cybernetics Inc., Rockville, MD, US).

Plant functional traits

We considered 11 plant functional traits that may reflect the ability of plant species to colonize landslides under a semi-arid climate (Table 2).

Table 2 Descriptions and data sources of the 11 plant functional traits

Plant functional trait	Scale; unit	Ecological implication	Data sources
Life span	Categorical; long-lived (more than five-year perennials) vs. short-lived (annuals, biennials and less than five-year perennials)	The longevity of the individual is the most basic trait that can enhance population persistence after plants become established (Weiher et al. 1999).	Field observations; literature[a]
Growth form	Categorical; woody (trees, shrubs and subshrubs) vs. herbaceous	Woodiness has been associated with plant persistence under disturbance (e.g., soil erosion and herbivory) after plants become established (Guàrdia 1995).	Field observations; literature[a]
Plant height (maximum height)	Continuous; cm	It has usually been associated with competitive vigor under resource stresses, and with the whole plant fecundity that can enhance population persistence after plants become established (Pérez-Harguindeguy et al. 2013).	Field measurements
Clonality	Categorical; clonality (plants with stolons, rhizomes, bulbils, tubers and turions, corms, tuberous roots, suckers, lignotuber and layering) vs. non-clonality (clonal organs absent)	Clonal behavior can give plants a short-distance opportunity to expand to new sites, and may be an effective means of colonization under circumstances of poor seed dispersal or limited seedling recruitment; clonality can also enhance population persistence after plants become established (Guerrero-Campo et al. 2008; Pérez-Harguindeguy et al. 2013).	Field observations; literature[b]
Seed production	Categorical; ≥ 1000 vs. 100–999 vs. < 100 seeds individual^{-1}	High seed production can give plants more opportunities to recruit, thus enhancing colonization and population persistence after plants become established (Bochet et al. 2009).	Field observations; literature[c]
Seed dispersal mode	Categorical; long-distance dispersal (anemochory and zoochory) vs. short-distance dispersal (barochory, autochory, ballistichory and myrmecochory)	Long-distance dispersal can give plants more opportunities to colonize at new sites and to exploit their patches once established (Bochet et al. 2009).	Laboratory observations; literature[d]
Seed mass	Continuous; mg	Small seeds are associated with large seed production; anemochorous seeds tend to be light in mass; small seeds tend to persist in soil seed banks; stored resources in heavy seeds tend to help seedlings to survive and establish under resource stresses (Pérez-Harguindeguy et al. 2013).	Laboratory measurements; literature[c]
Seed anchorage	Categorical; anchorage (trypanocarpy and myxospermy) vs. non-anchorage (atelechory)	Seeds with anchorage mechanisms can reduce post-dispersal removal by soil erosion and predation (García-Fayos et al. 2013).	Laboratory observations and experiments; literature[c]
Seed germination rate	Continuous; %	A high rate of germination is the beginning of a successful establishment and can also enhance population persistence after establishment (Weiher et al. 1999; Jiménez-Alfaro et al. 2016).	Laboratory experiments
Seed first germination	Continuous; days	Seeds with a short time for first germination can use limited water when soil water is available in a very short period of time, which is important for establishment and persistence in water-stressed environments (García-Fayos et al. 2000; Jiménez-Alfaro et al. 2016).	Laboratory experiments
Resprouting capacity	Categorical; resprouting (sprouts can be rhizomes, stems and lignotubers) vs. non-resprouting (sprouts absent)	Species with the resprouting capacity are able to recover and persist after disturbances (Pérez-Harguindeguy et al. 2013).	Field observations; literature[b]

[a] ECCAS (2004); [b] Chen et al. (2001); [c] Wang (2014); [d] Wang (2013)

We only used plant species that represented more than 80% of the cumulated abundance in each of the two landslide zones and the surrounding vegetated areas because they collect the largest source of functional variation of the vegetation (Pakeman and Quested 2007), resulting in a list of 71 out of the 112 plant species appeared on landslides and the surrounding vegetated areas. For these plant species we determined the categorical traits through field or laboratory observation and literature search and measured the continuous traits through field or laboratory experiments (Table 2).

We took plant samples from healthy mature individuals living in full light in the study area. For maximum height, we measured foliage heights of at least 25 individuals of each plant species. For clonality and resprouting capacity, we excavated at least five individuals of each plant species and looked for plant organs such as rhizomes, suckers and lignotubers. A plant species was considered clonal when we found several individuals interconnected through stems or roots (Pérez-Harguindeguy et al. 2013). A plant species was considered as a sprouter when we found that it retained old dead stems at the same time that new shoots were emerging aboveground from the same individual (Pérez-Harguindeguy et al. 2013). For the seed traits, we collected 10 seeds from each of 20 individuals of each plant species in each of five different sites. For seed mass, 50 oven-dry seeds (after removing seed appendages and drying at 80 °C for 48 h) of each plant species were weighed using an analytical balance (BS 224 S; Sartorius Scientific Instruments (Beijing) Co., Ltd., Beijing, China) with 0.1 mg precision. Germination tests were performed in a growth chamber (RXZ-380C; Ningbo Jiangnan Instrument Plant, Ningbo, China) with a humidity of 60% at 25 °C (13 h; 8800 lx illumination) and 16 °C (11 h; darkness). The humidity, temperatures, photoperiod length and illumination intensity mimic the average field conditions during the growing season in the area (Wang 2014). We used four Petri dishes for each plant species, each containing 50 seeds evenly put on two-layer filter paper constantly moistened by double distilled water. A seed was considered germinated when the radicle emerged from the seed coat (Fenner and Thompson 2005). The number of germinated seeds in each Petri dish was recorded every day for 30 days. Finally, we calculated seed germination rate (the average percentage of germinated seeds within the 30 days) and seed germination speed (the average number of days for the first germination within the 30 days) of each plant species. In addition, the presence of mucilage secretion of seeds, known as an anchorage mechanism of seeds (García-Fayos et al. 2013), was identified microscopically for each plant species during the germination tests.

Soil properties

We considered eight soil properties that may affect seed fixation and plant persistence on landslides and reflect the availability of soil water and nutrients of landslides for plant establishment and population persistence (Table 3).

Soil sampling was conducted in landslides 1 to 18 (representing 60% of the 30 landslides) and the surrounding vegetated areas in mid-April 2015 (the early growing season in the area). For each of the two landslide zones and the surrounding vegetated areas, we decided to sample to a depth of 5 cm because over 85% of seeds and most of the root biomass of seedlings can be found there (Chen et al. 2001; Wang et al. 2011b); then we took three soil samples, each comprising six evenly-distributed cores (height = 5 cm, diameter = 4.80 cm), to determine clay to sand ratio, organic matter content, inorganic nitrogen content and available phosphorus content, and we sampled another three evenly-distributed cores (height = 5 cm, diameter = 5.05 cm) to determine bulk density and available water content. The clay and sand particle counts were determined using a particle size analyzer (Mastersizer 2000; Malvern Instruments Co., Ltd., Malvern, UK). Bulk density was determined gravimetrically in the laboratory. Available water content is the difference between soil moisture content at field capacity (moisture content at 0.3 bar) and that at wilting point (moisture content at 15 bar), which were obtained from the water retention curve determined using a centrifuge (himac CR 21; Hitachi Co., Ltd., Tokyo, Japan) and then fitted using the RETC software (version 6.02, University of California, Riverside (UCR), California, US). Organic matter, inorganic nitrogen and available phosphorus contents were determined using the oil bath-$K_2Cr_2O_7$ titration method, a discrete analyzer (CleverChem 200$^+$; DeChem-Tech. GmbH, Hamburg, Germany) and the Olsen method with an ultraviolet photometer (UV-1600; Shanghai Meipuda Instrument Co., Ltd., Shanghai, China), respectively.

Table 3 Descriptions of the eight soil properties

Soil property	Unit	Ecological relevance
Slope angle	°	It is considered as a surrogate of soil erosion rate that can influence seed fixation and plant persistence on hillslopes (Cerdà and García-Fayos 1997; Bochet et al. 2009).
Clay to sand ratio		It is considered as a surrogate of the extent of seed-soil contact that can influence seed fixation (García-Fayos et al. 2013).
Bulk density	g cm^{-3}	It is considered as a surrogate of the possibility of runoff generation that can influence seed fixation (García-Fayos et al. 2013). It also indicates soil compactness that can influence seedling growth and root anchorage and elongation (Bulmer and Simpson 2005; Scott et al. 2005; Valentine et al. 2012).
Available water	mm^{-3} mm^{-3}	It refers to the maximum amount of water that can be stored in soil capillary pores and then absorbed by plants (Lin 2002).
Soil moisture	mm^{-3} mm^{-3}	It reflects the availability of soil water for plants at a moment (Lin 2002), thus influencing seed germination, seedling survival, and the vegetative and reproductive growth of adult plants (García-Fayos et al. 2000; Fenner and Thompson 2005; Bochet et al. 2007; Gorai et al. 2015).
Organic matter Inorganic nitrogen (Ammonium and nitrate) Available phosphorus	g kg^{-1} mg kg^{-1} mg kg^{-1}	The richness of soil organic matter and these soil nutrients can influence seedling survival and the vegetative and reproductive growth of adult plants (Fetcher et al. 1996; Walters and Reich 2000; Shiels et al. 2006; Moraes et al. 2016).

We also measured soil moisture dynamics in eight selected landslides (landslides 5, 6, 7, 8, 11, 12, 15 and 18) and the surrounding vegetated areas in the Yaozigou watershed. We selected these landslides in a single watershed in order to prevent differences in soil moisture dynamics derived from the spatially heterogeneous distribution of rain during storms. For each of the two landslide zones and the surrounding vegetated areas, TDR sensors (TRIME-PICO 64; IMKO Micromodultechnik GmbH, Esslingen, Germany) were used at three evenly-distributed permanent points to a depth of 5 cm in the middle of each month from April to October (within the growing season in the area) in 2015 and 2016.

Data analysis

To quantify general vegetation changes after landslides, we analyzed differences among scars, deposits and the surrounding vegetated areas in vegetation cover and species richness using generalized linear mixed models (GLMMs). Site was considered as a fixed factor with three levels, i.e., scar, deposit and the surrounding vegetated area. Landslide identity was considered as a random factor, giving the spatial interdependence of the two zones of each landslide and the surrounding vegetated area. For vegetation cover, we used a normal distribution with a power link; for species richness, we used a poisson distribution with a log link. Least significant difference (LSD) tests were used for post hoc multiple comparisons among the three geomorphologic classes. Analyses were performed using SPSS (IBM SPSS Statistics 20.0; International Business Machines Corporation, Armonk, New York, US). To quantify changes in plant species composition after landslides, we applied non-metric multidimensional scaling (NMDS) to the data on species abundance of the 30 landslides and the surrounding vegetated areas. This ordination method has been commonly considered as the most robust unconstrained ordination method in plant community ecology, and the smaller the “stress” value is, the lower the degree of distortion of the original dissimilarity values among species composition of sampling sites becomes (Oksanen et al. 2016). We used the “metaMDS” function of the “vegan” package written for R 3.3.2 (R Core Team 2017) and selected the Bray-Curtis index as a dissimilarity index.

For each of the two landslide zones and the surrounding vegetated areas, we calculated the community-weighted mean (CWM; Garnier et al. 2004) of each of the 11 plant functional trait (weighted by the relative abundance of the plant species that represented more than 80% of the cumulated abundance). We assigned two values, i.e., 1 and 0, to the first and second classes of each categorical trait, respectively (see Table 2), but for seed production, we assigned three values, i.e., 1000, 100 and 10, to the three classes ≥1000, 100–999 and <100 seeds individual^{-1}, respectively. To quantify trait changes after landslides, we analyzed differences among scars, deposits and the surrounding vegetated areas in the CWMs of the 11 plant functional traits using GLMMs. For life span, clonality, seed dispersal mode, seed anchorage, seed germination rate, seed first germination and resprouting capacity, we used a normal distribution with an identity link; for plant height and seed production, we used a normal distribution with a log link; and for growth form and seed mass, we used a normal distribution with a power link.

To quantify soil changes after landslides, we first analyzed differences among scars, deposits and the surrounding vegetated areas in the seven physical and chemical properties using GLMMs. For bulk density and available water, we used a normal distribution with an identity link; for slope angle, clay to sand ratio, organic matter and inorganic nitrogen, we used a normal distribution with a log link; and for available phosphorus, we used a normal distribution with a power link. Then, we analyzed differences among the three geomorphologic classes in soil moisture using GLMMs with a repeated measures structure, considering repeated measurement as a within-subject factor. For soil moisture within the growing season of 2016, we used a normal distribution with an identity link; for soil moisture within the growing season of 2015, we used a normal distribution with a log link. In addition, we used the Mantel test to test whether soil properties were spatially correlated because our studied landslides are unevenly distributed in the study area. First, we standardized the values of soil variables (excluding soil moisture) in each of the two zones of the 18 landslides and the surrounding vegetated areas using the "chi.square" command of the "vegan" package, and we calculated a dissimilarity matrix of the soil variables among sites of the 18 landslides based on the Bray-Curtis index of the "vegan" package. Then, we calculated the inverse matrix of the geographic distances among sites of the 18 landslides. And last, we used the "mantel" command of the "vegan" package to quantify the correlation between the two matrices.

To identify the soil properties that could drive post-landslide changes in plant species composition, we fitted soil vectors (excluding soil moisture) onto an abundance-based NMDS ordination of the 18 landslides and the surrounding vegetated areas for which we had data on both plant species abundance and soil variables using the "envfit" function of the "vegan" package. Furthermore, to identify the plant functional traits that could reflect post-landslide changes in plant species composition, we fitted trait vectors onto the abundance-based NMDS ordination of the 30 landslides and the surrounding vegetated areas using the same function.

Results

Vegetation properties

We found that the vegetation cover of scars was significantly lower than those of deposits and the surrounding vegetated areas, while species richness did not differ significantly among scars, deposits and the surrounding vegetated areas (fixed effect: $F_{2,\ 86} = 5.479$ and 0.188, respectively, and *p*-values = 0.006 and 0.829, respectively; see Table S2 for other relevant statistics) (Fig. 1).

Within the NMDS ordination space (Fig. 2), we found that the scar and the deposit of each landslide and the surrounding vegetated area appeared close to each other with few exceptions, and that scars, deposits and the surrounding vegetated areas were all not clustered and none of the three geomorphologic classes was separated from each other, indicating a higher degree of similarity among the three geomorphologic classes than among the sites within each geomorphologic class.

Plant functional traits

We found that none of the 11 plant functional traits differed significantly among scars, deposits and the surrounding vegetated areas (fixed effect: for life span, growth form, plant height, clonality, seed production, seed dispersal mode, seed mass, seed anchorage, seed germination rate, seed first germination and resprouting capacity, $F_{2,\ 86} = 0.311$, 0.067, 0.040, 0.139, 0.090, 0.040, 0.066, 0.024, 0.001, 0.019 and 0.200, respectively, and *p*-values = 0.733, 0.936, 0.961, 0.870, 0.914, 0.961, 0.936, 0.976, 0.999, 0.981 and 0.819, respectively; see Table S3 for other relevant statistics) (Fig. 3).

When we fitted trait vectors onto the NMDS ordination (Fig. 2), we found that along the axis 1, plant species composition was positively correlated with

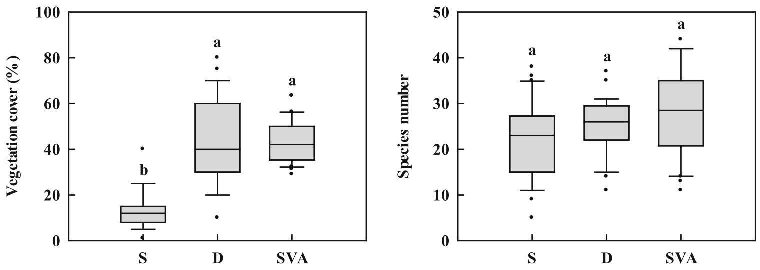


Fig. 1 Boxplots of values of vegetation cover and plant species richness of scars (S), deposits (D) and the surrounding vegetated areas (SVA) ($n = 30$). Different letters denote significant differences at the 0.05 level in the post-hoc LSD tests

growth form, plant height, seed production, seed mass, seed anchorage and seed germination rate (r-values = 0.485, 0.349, 0.308, 0.109, 0.165 and 0.175, respectively, and p-values = 0.001, 0.001, 0.001, 0.006, 0.002 and 0.002, respectively) and was negatively correlated with seed dispersal mode, days for seed first germination and resprouting capacity (r-values = −0.313, −0.230 and −0.371, respectively, and all p-values = 0.001); and along the axis 2, it was negatively correlated with life span (r-value = −0.154, and p-value = 0.001).

Soil properties

We found that scars were significantly steeper than deposits and the surrounding vegetated areas, while clay to sand ratio, bulk density, available water, organic matter, inorganic nitrogen and available phosphorus did not differ significantly among scars, deposits and the surrounding vegetated areas (fixed effect: $F_{2,\ 50}$ = 3.495, 0.430, 1.314, 0.005, 1.643, 0.101 and 0.017, respectively, and p-values = 0.038, 0.653, 0.278, 0.995, 0.204, 0.904 and 0.983, respectively; see Table S4 for other relevant statistics) (Fig. 4).

We also found that soil moisture in 0–5 cm layer did not differ significantly among scars, deposits and the surrounding vegetated areas within the growing seasons of 2015 and 2016 (fixed effect: $F_{2,\ 158}$ = 0.056 and 0.284, respectively, and p-values = 0.946 and 0.753, respectively; see Table S4 for other relevant statistics) (Fig. 5).

In addition, we found that the soil properties (excluding soil moisture) were not spatially correlated (r_{mantel} = 0.007, and p-value = 0.357).

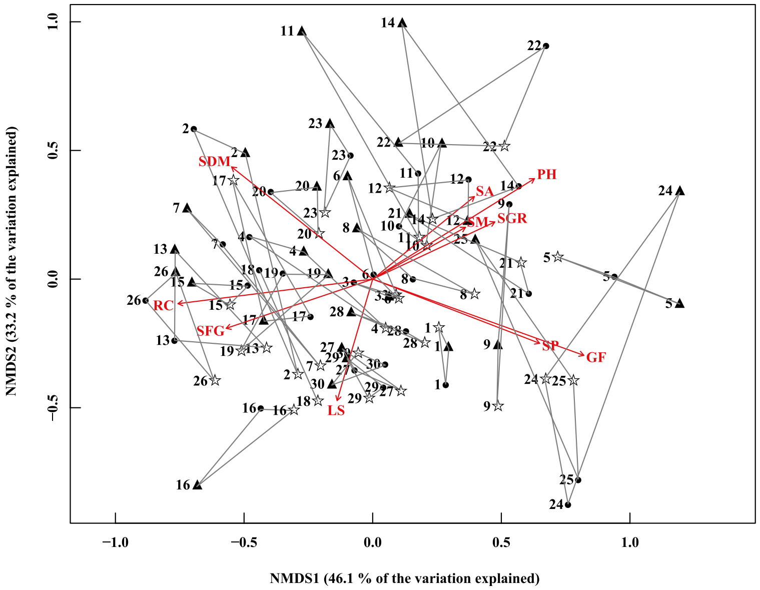


Fig. 2 NMDS ordination graph based on species abundance of the two zones of the 30 landslides and the surrounding vegetated areas with the presentation of the CWMs of the trait variables that were significantly correlated with plant species composition at the 0.05 level ($n = 30$; stress value = 0.240). Numbers denote landslides, and circles, triangles and stars denote scars, deposits and the surrounding vegetated areas, respectively. The two zones of each landslide and the surrounding vegetated area were linked with gray solid lines. LS, GF, PH, SP, SDM, SM, SA, SGR, SFG and RC denote life span, growth form, plant height, seed production, seed dispersal mode, seed mass, seed anchorage, seed germination rate, seed first germination and resprouting capacity, respectively

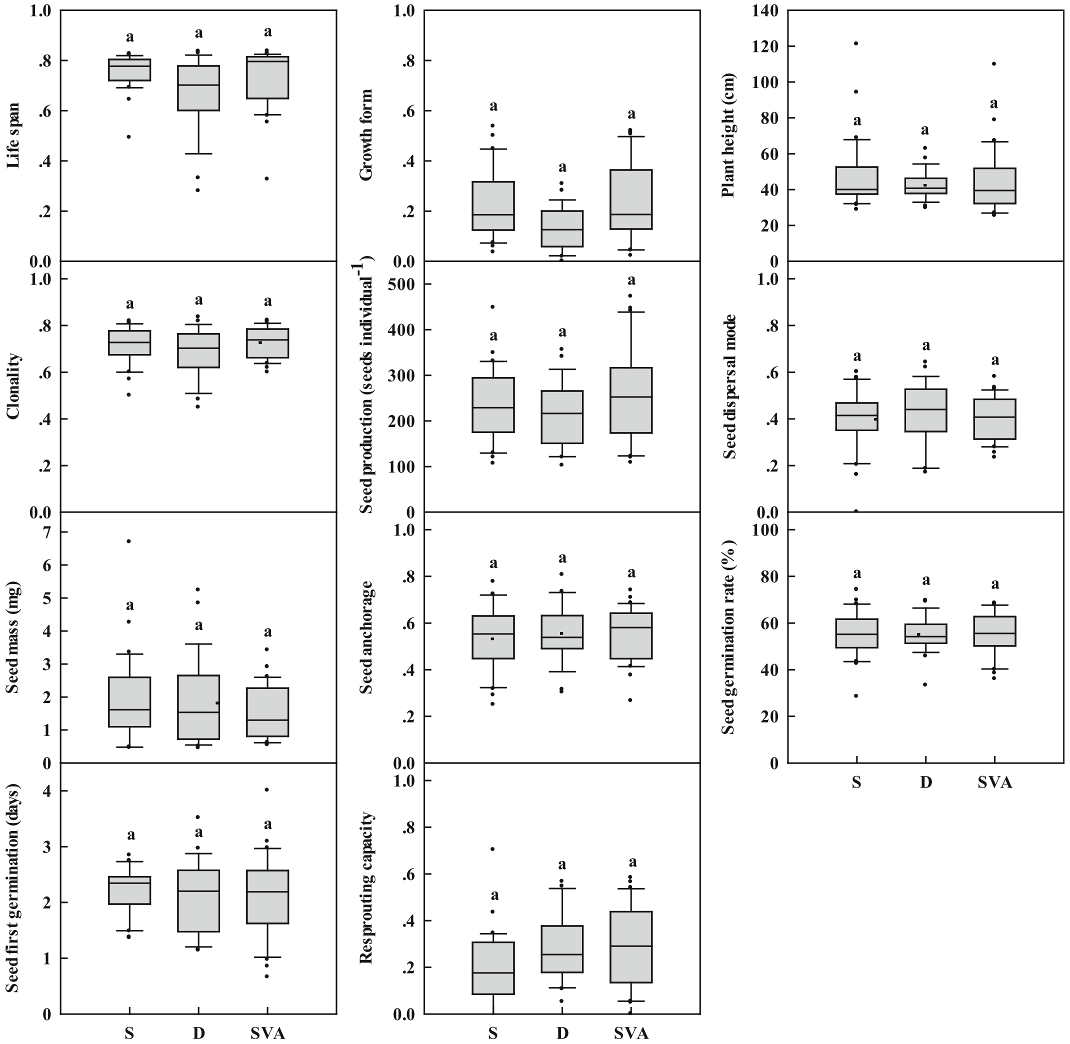


Fig. 3 Boxplots of the CWMs of the plant functional traits in scars (S), deposits (D) and the surrounding vegetated areas (SVA) ($n = 30$). Different letters denote significant differences at the 0.05 level in the post-hoc LSD tests

When we fitted soil vectors (excluding soil moisture) onto the NMDS ordination of the 18 landslides (Fig. 6), we found that along the axis 1, plant species composition was positively correlated with soil available phosphorus content (r-value = 0.155, and p-value = 0.015) and was negatively correlated with soil clay to sand ratio and available water content (r-values = −0.299 and −0.133, respectively, and p-values = 0.001 and 0.027, respectively).

Discussion

In this study, we hypothesized that under a semi-arid climate, landslides would exert profound effects on soil properties and then on vegetation properties, and that plant-soil interactions during plant recolonization could be revealed through post-landslide changes in plant functional traits. However, our findings did not fit the hypothesis.

First, we found that soil physical properties, soil moisture and soil fertility did not differ significantly between landslides and the surrounding vegetated areas and between scars and deposits (Figs. 4 and 5), in contrast with most of the reported soil changes after landslides under other climate regimes, where soils after landslides typically become much more compact, arid and infertile compared with the surrounding undisturbed substrates, and within landslides, soils of scars are much more infertile than those of deposits (Adams and Sidle 1987;

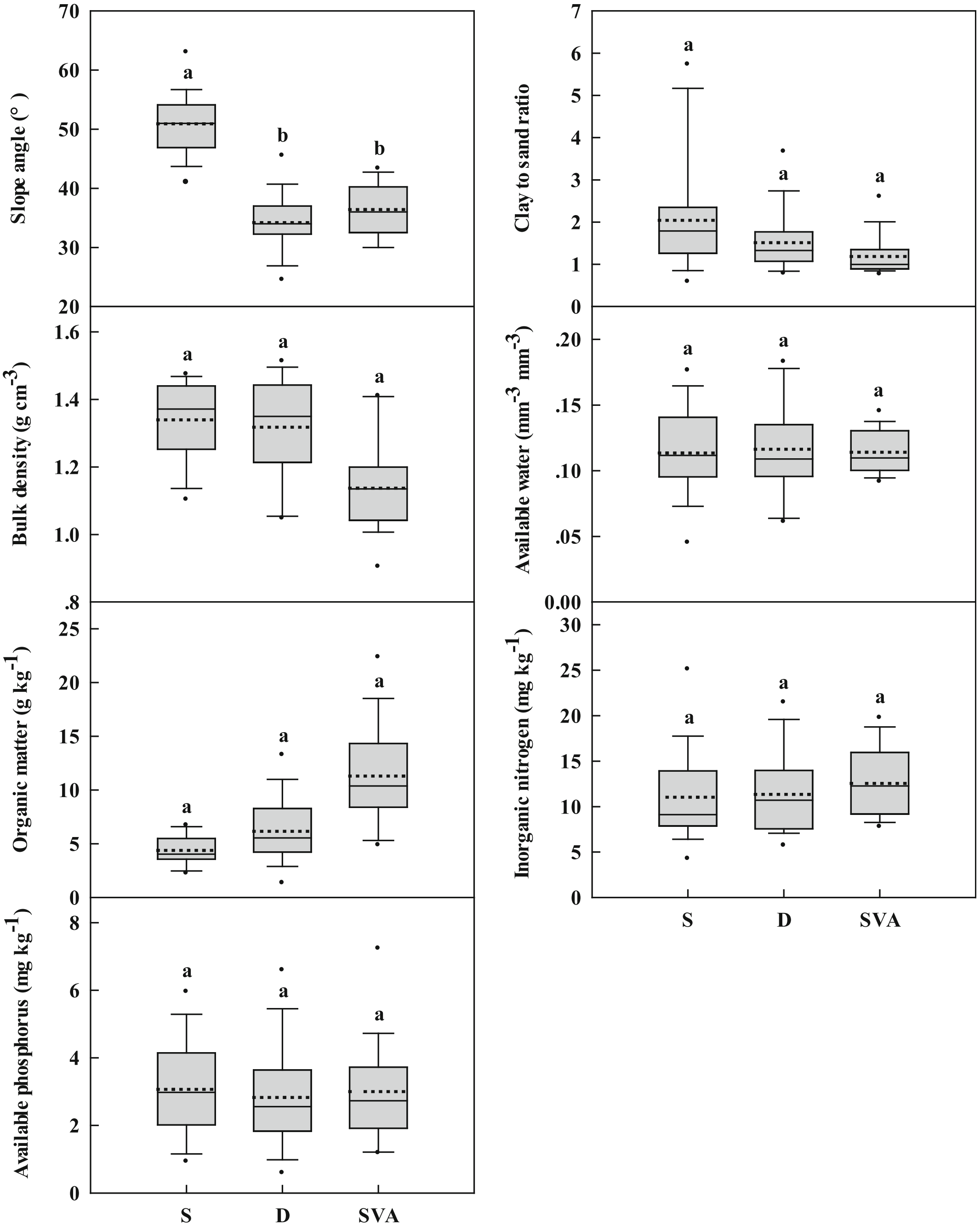
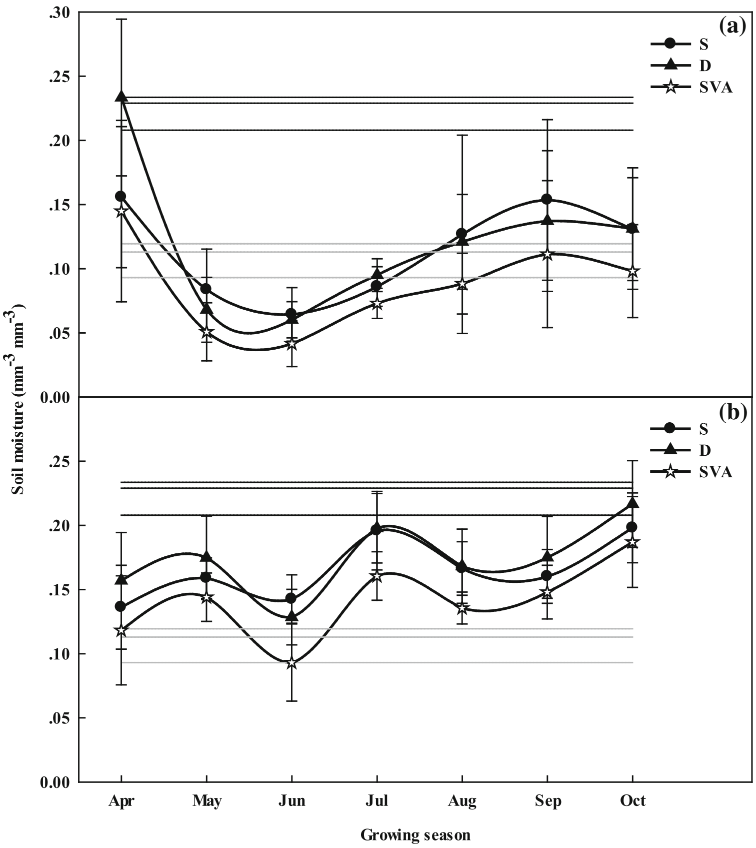


Fig. 4 Boxplots of the values of the soil properties of scars (S), deposits (D) and the surrounding vegetated areas (SVA) (*n* = 18). Different letters denote significant differences at the 0.05 level in the post-hoc LSD tests

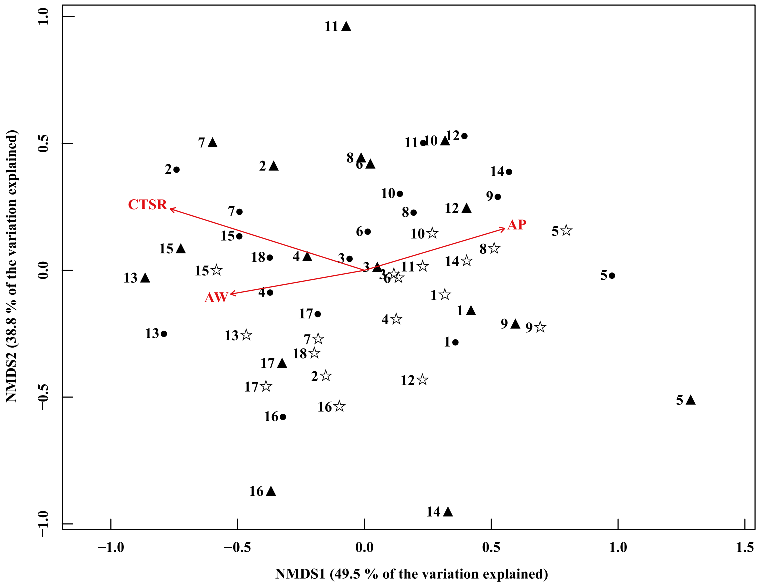
Guariguata 1990; Dalling and Tanner 1995). However, the lack of changes in soil properties after landslides in our study area can be explained from the perspective of pedogenesis. Huang (2011) reported that until 500 cm depth, the soil profile in the area is homogeneous in clay mineral composition and $CaCO_3$ content, corresponding to homogenous deposition and formation of the loess within the last 11,500 years; and that high $CaCO_3$ content and extremely low magnetic susceptibility of the soil profile indicate that a cold semi-arid climate has been

Fig. 5 Soil moisture dynamics in 0–5 cm layer in scars (S), deposits (D) and the surrounding vegetated areas (SVA) within the growing seasons of (**a**) 2015 and (**b**) 2016 ($n = 8$). Black solid horizontal lines from above to below denote the respective field capacities of scars, deposits and the surrounding vegetated areas, and gray solid horizontal lines from above to below denote the respective wilting points of scars, deposits and the surrounding vegetated areas. Soil moisture is available for plants only when its value is between field capacity and wilting point (Lin 2002)



prevailing all the time and leads to comparatively slow formation of the loess in the area. From this depth downwards, there may be a substantial change to more ancient soils, i.e., Lishi loess and Wucheng loess, which were formed during the Pleistocene and have distinctive physical and chemical properties (Liu and Ding 2004). Since

Fig. 6 NMDS ordination graph based on species abundance of the two zones of the 18 landslides and the surrounding vegetated areas with the presentation of the soil variables that were significantly correlated with plant species composition at the 0.05 level ($n = 18$; stress value = 0.224). Numbers denote landslides, and circles, triangles and stars denote scars, deposits and the surrounding vegetated areas, respectively. AP, CTSR and AW denote available phosphorus, clay to sand ratio and available water, respectively



our studied landslides (<50 cm erosion depth) were not deep enough to erode the deep-seated Lishi loess or even Wucheng loess, the topsoil that we sampled from scars, deposits and the surrounding vegetated areas should have no critical differences.

Second, in accordance with previous research (Lundgren 1978; Velázquez and Gómez-Sal 2007), we found that scars were significantly steeper than the surrounding vegetated areas, and within landslides, scars were significantly steeper than deposits (Fig. 4). The potentially filtering effect of slope angle on plant recolonization following landslides has been identified, largely as a consequence of intensified soil erosion on the newly exposed soil surfaces (Wilcke et al. 2003; Shiels et al. 2008; Walker et al. 2013). Thus, in our study area, slope angle was expected to be a potential filter on scars, filtering or restricting the plant species whose seeds or individuals have difficulties with persistence. In contrast, deposits were expected to be a species reservoir because of their gentler slopes.

Despite these expectations, we found that plant species richness and composition did not perceptibly varied between landslides and the surrounding vegetated areas and between scars and deposits (Figs. 1 and 2), in a stark contrast with the reported vegetation changes after landslides under other climate regimes, where the surrounding rare or minor species or even exotic species can remarkably increase their abundance on landslides, by the relevance with the exposure of underlying soil caused by landslides (Restrepo and Vitousek 2001; Neto et al. 2017), and within landslides, several species are much more abundant or frequent on deposits than on scars, partly because of the presence of remaining soil (Guariguata 1990; Velázquez and Gómez-Sal 2007). Furthermore, the lack of changes in plant species richness and composition after landslides in our study area suggests that the surrounding plant species will not be strongly filtered by (the steepest) scars, nor by (the gentle) deposits, and both scars and deposits can hardly change the relative abundance of colonizing species relative to their abundance in the surrounding vegetated areas. This suggestion is also supported by the findings that none of the plant functional traits differed significantly between landslides and the surrounding vegetated areas and between scars and deposits (Fig. 3). Another convincing proof is that the soil properties (slope angle in particular) and plant traits (growth form, seed mass, seed anchorage and resprouting capacity in particular) had weak correlations with plant species composition (all the correlation coefficients <0.500; Yu and He 2003), and more importantly, that none of them could differentiate between landslides and the surrounding vegetated areas and between scars and deposits along the NMDS ordination axes (Figs. 2 and 6), in other words, there were no soil properties that could drive changes in plant species composition after landslides, nor plant functional traits that could reflect the expected changes in plant species composition.

It is not difficult to understand the lack of vegetation and trait changes after landslides in our study area. Huang (2011) found that a cold semiarid climate has been lasting for 11,500 years since the Holocene in the area. Landslides have also been occurring in the area for millennia as a consequence of slope regularization and human activities (Liu and Wu 1996; Li et al. 2008). Therefore, we may realize that the current regional species pool should have been composed of the species whose traits reflect higher fitness for the climate conditions as well as the soil conditions of landslides. We may further predict that plant species inhabiting the area could colonize not only shallow-seated landslides but also deep-seated landslides without much difficulty. This is an interesting prediction that remains to be tested.

In terms of vegetation cover, we found that, two years after landslides, deposits had approached the value of the surrounding vegetated areas, while the value of scars was significantly lower than those of deposits and the surrounding vegetated areas (Fig. 1). These findings are in agreement with those reported for landslides in the Franconia Notch of US, where the vegetation recovery of scars tends to be tardy relative to that of deposits (Francescato et al. 2001). This within-landslide difference in the speed of vegetation recovery in our study area can be interpreted from a biological perspective. Landslides often leave lots of available seeds, sprouts and plants to deposits but leave scarcely any biological legacies to scars (Guariguata 1990; Restrepo et al. 2009). Therefore, in our study area, deposits probably had a head start over scars in terms of vegetation recovery just after landslide formation and thus could be revegetated comparatively quickly. Despite this difference, the vegetation recovery of scars should be only a matter of time because most of the surrounding species have already appeared on scars just two years after landslides (Fig. 2 and Table S5).

Although our findings did not fit our hypothesis, they highlight the restoration potential of our studied landslides and the resistance of our slope ecosystems to landslide disturbance. First, species richness was not strongly reduced because of landslide formation (Fig. 1). Second, with few exceptions, species composition on the two-year-old scars and deposits had approached that on the surrounding vegetated areas (Fig. 2), and more importantly, the most abundant species in whether the surrounding vegetated areas or the two-year-old scars and deposits were almost the same (Table S5). These findings indicate that the surrounding plant species play an important role in providing available propagules for landslides, especially for scars, and that neither scars nor deposits have to experience a long-term succession process to approach the surrounding species composition. Third, deposits only took two years to approach the surrounding vegetation cover (Fig. 1). A similar restoration potential has been reported for landslides in the Mgeta Valley of western Uluguru Moutains of Tanzania (Lundgren 1978), but other landslides, such as those in the Luquillo Experimental Forest (subtropical lower montane wet forest) on the upper Luquillo Mountains of Puerto Rico may require at least 50 years to approach the mature-forest species composition (Guariguata 1990) and those in the Ninole ridges on the island of Hawai'i of USA may require at least 130 years to resemble the undisturbed-forest species composition (Restrepo and Vitousek 2001).

In conclusion, under the semi-arid climate of the area, landslides do not have profound effects on soil properties and plant species richness and composition, telling a different story from those landslides under other climate regimes and implying great potential for the restoration of landslides and the resistance of slope ecosystems to landslide disturbance in the area. We may propose that a huge investment in restoration measures for landslides in the area is not necessary.

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References

Adams PW, Sidle RC (1987) Soil conditions in three recent landslides in Southeast Alaska. For Ecol Manage 18:93–102

Arnáez J, Lana-Renault N, Ruiz-Flaño P, Pascual N, Lasanta T (2017) Mass soil movement on terraced landscapes of the Mediterranean mountain areas: a case study of the Iberian range, Spain. Cuadernos de Investigación Geográfica 43:83–100

Bochet E (2015) The fate of seeds in the soil: a review of the influence of overland flow on seed removal and its consequences for the vegetation of arid and semiarid patchy ecosystems. Soil 1:131–146

Bochet E, García-Fayos P, Alborch B, Tormo J (2007) Soil water availability effects on seed germination account for species segregation in semiarid roadslopes. Plant Soil 295:179–191

Bochet E, García-Fayos P, Poesen J (2009) Topographic thresholds for plant colonization on semi-arid eroded slopes. Earth Surf Proc Land 34:1758–1771

Bulmer CE, Simpson DG (2005) Soil compaction and water content as factors affecting the growth of lodgepole pine seedlings on sandy clay loam soil. Can J Soil Sci 85:667–679

Cao BT, Jiao JY, Wang ZJ, Wei YH, Li YJ (2015) Characteristics of landslide under the extreme rainstorm in 2013 in the Yanhe basin. Research of Soil and Water Conservation 22: 103–109 [In Chinese]

Cerdà A, García-Fayos P (1997) The influence of slope angle on sediment, water and seed losses on badland landscapes. Geomorphology 18:77–90

Chen SH, Zhang H, Wang LQ, Zhan BL, Zhao ML (2001) Root systems of plants on the grassland in North China. Jilin University Press, Changchun [In Chinese]

Dalling JW (1994) Vegetation colonization of landslides in the Blue Mountains, Jamaica. Biotropica 26:392–399

Dalling JW, Tanner EVJ (1995) An experimental study of regeneration on landslides in montane rain forest in Jamaica. J Ecol 83:55–64

ECCAS (Editor Committee of the Chinese Academy of sciences for Flora of China) (2004) Flora of China. Science Press, Beijing [In Chinese]

Fenner M, Thompson K (2005) The ecology of seeds. Cambridge University Press, New York

Fetcher N, Haines BL, Cordero RA, Lodge DJ, Walker LR, Fernández DS, Lawrence WT (1996) Responses of tropical plants to nutrients and light on a landslide in Puerto Rico. J Ecol 84:331–341

Francescato V, Scotton M, Zarin DJ, Innes JC, Bryant DM (2001) Fifty years of natural revegetation on a landslide in Franconia notch, New Hampshire, U.S.A. Can J Bot 79:1477–1485

García-Fayos P, García-Ventoso B, Cerdà A (2000) Limitations to plant establishment on eroded slopes in southeastern Spain. J Veg Sci 11:77–86

García-Fayos P, Engelbrecht M, Bochet E (2013) Post-dispersal seed anchorage to soil in semiarid plant communities, a test of the hypothesis of Ellner and Shmida. Plant Ecol 214:941–952

Garnier E, Cortez J, Billès G, Navas ML, Roumet C, Debussche M, Laurent G, Blanchard A, Aubry D, Bellmann A, Neill C, Toussaint JP (2004) Plant functional markers capture ecosystem properties during secondary succession. Ecology 85:2630–2637

Gorai M, Laajili W, Santiago LS, Neffati M (2015) Rapid recovery of photosynthesis and water relations following soil drying and re-watering is related to the adaptation of desert shrub *Ephedra alata* subsp. *alenda* (Ephedraceae) to arid environments. Environ Exp Bot 109:113–121

Guàrdia R (1995) La colonització vegetal de les áreas erosionades de la conca de la Baells (Alt Llobregat). [Plant colonization of eroded areas in the Baells watershed (Alt Lobregat, Spain)]. Dissertation, Universitat de Barcelona [In Spanish]

Guariguata MR (1990) Landslide disturbance and forest regeneration in the upper Luquillo Mountains of Puerto Rico. J Ecol 78:814–832

Guerrero-Campo J, Palacio S, Montserrat-Martí G (2008) Plant traits enabling survival in Mediterranean badlands in northeastern Spain suffering from soil erosion. J Veg Sci 19:457–464

Guo Z, Huang ZL, Feng LX (1992) Shaanxi soils. Science Press, Beijing [In Chinese]

Huang CQ (2011) Clay minerals in loess on the Loess Plateau and its environmental significance. Dissertation, University of Chinese Academy of Sciences [In Chinese]

Jiménez-Alfaro B, Silveira FAO, Fidelis A, Poschlod P, Commander LE (2016) Seed germination traits can contribute better to plant community ecology. J Veg Sci 27:637–645

Köppen W (1884) The thermal zones of the earth according to the duration of hot, moderate and cold periods and the impact of heat on the organic world. Meteorol Z 1:215–226

Lepš J, de Bello F, Lavorel S, Berman S (2006) Quantifying and interpreting functional diversity of natural communities: practical considerations matter. Preslia 78:481–501

Li R, Yang WZ, Li BC (2008) Research and Future Prospects for the Loess Plateau of China. Science Press, Beijing [In Chinese]

Lin DY (2002) Soil science. China Forestry Press, Beijing [In Chinese]

Liu DS, Ding ML (2004) The Loess Plateau, the origin of agriculture, and water and soil conservation. Seismological Press, Beijing [In Chinese]

Liu BZ, Wu FQ (1996) Soil erosion. Shaanxi people's Publishing House, Xi'an [In Chinese]

Lozano P, Bussmann RW (2005) Importancia de los deslizamientos en el Parque Nacional Podocarpus, Loja-Ecuador. [Importance of landslides in Podocarpus National Park, Loja-Ecuador]. Revista Peruana de Biologia 12: 195–202 [In Spanish]

Lundgren L (1978) Studies of soil and vegetation development on fresh landslide scars in the Mgeta Valley, western Uluguru Mountains, Tanzania. Geografiska Annaler. Geogr Ann A 60: 91–120

Moraes DA, Cavalin PO, Moro RS, Oliveira RAC, Carmo MRB, Marques MCM (2016) Edaphic filters and the functional structure of plant assemblages in grasslands in southern Brazil. J Veg Sci 27:100–110

Myster RW, Femández DS (1995) Spatial gradients and patch structure on two Puerto Rican landslides. Biotropica 27: 149–159

Neto C, Cardigos P, Oliveira SC, Zezere JL (2017) Floristic and vegetation successional processes within landslides in a Mediterranean environment. Sci Total Environ 574:969–981

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H (2016) Vegan: Community Ecology Package. v. 2.4–1. https://CRAN.Rproject.org/package=vegan

Pakeman RJ, Quested HM (2007) Sampling plant functional traits: what proportion of the species need to be measured? Appl Veg Sci 10:91–96

Pérez-Harguindeguy N, Díaz S, Garnier E, Lavorel S, Poorter H, Jaureguiberry P, Bret-Harte MS, Cornwell WK, Craine JM, Gurvich DE, Urcelay C, Veneklaas EJ, Reich PB, Poorter L, Wright IJ, Ray P, Enrico L, Pausas JG, de Vos AC, Buchmann N, Funes G, Quétier F, Hodgson JG, Thompson K, Morgan HD, ter Steege H, van der Heijden MGA, Sack L, Blonder B, Poschlod P, Vaieretti MV, Conti G, Staver AC, Aquino S, Cornelissen JHC (2013) New handbook for standardised measurement of plant functional traits worldwide. Aust J Bot 61:167–234

R Core Team (2017) R: A Language and Environment for Statistical Computing. (v. 3.3.2) R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Record S, Kobe RK, Vriesendorp CF, Finley AO (2016) Seedling survival responses to conspecific density, soil nutrients, and irradiance vary with age in a tropical forest. Ecology 97: 2406–2415

Restrepo C, Vitousek P (2001) Landslides, alien species and the diversity of a Hawaiian montane mesic ecosystem. Biotropica 33:409–422

Restrepo C, Vitousek P, Neville P (2003) Landslides significantly alter land cover and the distribution of biomass: an example from the Ninole ridges of Hawai'i. Plant Ecol 166:131–143

Restrepo C, Walker LR, Shiels AB, Bussmann R, Claessens L, Fisch S, Lozano P, Negi G, Paolini L, Poveda G, Ramos-Scharrón C, Richter M, Velázquez E (2009) Landsliding and its multiscale influence on mountainscapes. Bio Sci 59:685–698

Scott DI, Tams AR, Berry PM, Mooney SJ (2005) The effects of wheel-induced soil compaction on anchorage strength and resistance to root lodging of winter barley (*Hordeum vulgare* L.) Soil Till Res 82:147–160

Shiels AB, Walker LR, Thompson DB (2006) Organic matter inputs create variable resource patches on Puerto Rican landslides. Plant Ecol 184:223–236

Shiels AB, West CA, Weiss L, Klawinski PD, Walker LR (2008) Soil factors predict initial plant colonization on Puerto Rican landslides. Plant Ecol 195:165–178

Sidle RC, Bogaarda TA (2016) Dynamic earth system and ecological controls of rainfall-initiated landslides. Earth-Sci Rev 159:275–291

Sidle RC, Ochiai H (2006) Landslides: processes, prediction, and land use. Am. Geophys. Union water Resour. Monogr. Vol. 18. American Geophysical Union, Washington, D.C., pp 312

Silvera K, Skillman JB, Dalling JW (2003) Seed germination, seedling growth and habitat partitioning in two morphotypes of the tropical pioneer tree *Trema micrantha* in a seasonal forest in Panama. J Trop Ecol 19:27–34

Valentine TA, Hallett PD, Binnie K, Young MW, Squire GR, Hawes C, Bengough AG (2012) Soil strength and macropore volume limit root elongation rates in many UK agricultural soils. Ann Bot-London 110:259–270

Velázquez E, Gómez-Sal A (2007) Environmental control of early succession on a large landslide in a tropical dry ecosystem (Casita Volcano, Nicaragua). Biotropica 39:601–609

Velázquez E, Gómez-Sal A (2008) Landslide early succession in a neotropical dry forest. Plant Ecol 199:295–308

Velázquez E, Gómez-Sal A (2009) Different growth strategies in the tropical pioneer tree *Trema micrantha* during succession on a large landslide on Casita Volcano, Nicaragua. J Trop Ecol 25:249–260

Walker LR, Shiels AB (2008) Post-disturbance erosion impacts carbon fluxes and plant succession on recent tropical landslides. Plant Soil 313:205–216

Walker LR, Shiels AB (2013) Landslide ecology. Cambridge University Press, Cambridge

Walker LR, Zarin DJ, Fetcher N, Myster RW, Johnson AH (1996) Ecosystem development and plant succession on landslides in the Caribbean. Biotropica 28:566–576

Walker LR, Velázquez E, Shiels AB (2009) Applying lessons from ecological succession to the restoration of landslides. Plant Soil 324:157–168

Walker LR, Shiels AB, Bellingham PJ, Sparrow AD, Fetcher N, Landau FH, Lodge DJ (2013) Changes in abiotic influences on seed plants and ferns during 18 years of primary succession on Puerto Rican landslides. J Ecol 101:650–661

Walters MB, Reich PB (2000) Seed size, nitrogen supply, and growth rate affect tree seedling survival in deep shade. Ecology 81:1887–1901

Wang N (2013) The limiting factors in vegetation recruitment in the hilly-gullied region of the Loess Plateau: on species resources aspect. Dissertation, University of Chinese Academy of Sciences [In Chinese]

Wang DL (2014) Seed life-history strategies of plants and restoration by seed addition in the hill-gully Loess Plateau region. Dissertation, Northwest A & F University [In Chinese]

Wang N, Jiao JY, Jia YF, Wang DL (2011a) Seed persistence in the soil on eroded slopes in the hilly-gullied loess plateau region, China. Seed Sci Res 21:295–304

Wang N, Jiao JY, Jia YF, Zhang XA (2011b) Soil seed bank composition and distribution on eroded slopes in the hill-gully loess plateau region (China): influence on natural vegetation colonization. Earth Surf Proc Land 36:1825–1835

Weiher E, van der Werf A, Thompson K, Roderick M, Garnier E, Eriksson O (1999) Challenging Theophrastus: a common core list of plant traits for functional ecology. J Veg Sci 10: 609–620

Wilcke W, Valladarez H, Stoyan R, Yasin S, Valarezo C, Zech W (2003) Soil properties on a chronosequence of landslides in montane rain forest, Ecuador. Catena 53:79–95

Xu ZJ, Lin ZG, Zhang MS (2007) Loess in China and loess landslides. Chinese Journal of Rock Mechanics and Engineering 26: 1297–1312 [In Chinese]

Yu JY, He XH (2003) Statistical analysis and SPSS application. Posts & Telecom Press, Beijing [In Chinese]

Zhang MS, Li TL (2011) Triggering factors and forming mechanism of loess landslides. J Eng Geol 19:530–540 [In Chinese]

Supplementary material (Tables S1–S5) for

Telling a different story: Plant species recolonization after landslides under a semiarid climate. *Plant Soil*

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Table S1 The areas of scars and deposits of the 30 landslides

Landslide number	Scar area (m^2)	Deposit area (m^2)	**Landslide number**	Scar area (m^2)	Deposit area (m^2)
1	15.0	25.0	**16**	36.5	107.5
2	60.0	94.5	**17**	67.0	48.0
3	60.4	70.0	**18**	44.0	-
4	52.8	55.0	**19**	97.5	48.0
5	143.0	140.0	**20**	33.8	81.3
6	45.0	20.0	**21**	21.0	34.0
7	50.0	18.0	**22**	40.5	81.0
8	35.0	36.0	**23**	21.5	56.4
9	42.0	48.0	**24**	45.0	28.0
10	24.0	21.2	**25**	34.3	43.5
11	22.5	12.0	**26**	88.0	39.0
12	42.0	37.5	**27**	64.8	33.0
13	60.2	48.0	**28**	52.0	31.5
14	24.0	16.0	**29**	27.9	29.0
15	42.0	28.0	**30**	60.0	32.0

Table S2 Multiple comparisons (LSD) in vegetation cover and species richness among scars (S), deposits (D) and the surrounding vegetated areas (SVA)

Vegetation property	*t*-value		$Pr(>\lvert t \rvert)$
Vegetation cover	t_{SVA-D}	0.089	0.930
	t_{SVA-S}	2.629	**0.010**
	t_{D-S}	2.547	**0.013**
Species richness	t_{SVA-D}	0.268	0.790
	t_{SVA-S}	0.605	0.547
	t_{D-S}	0.342	0.733

Table S3 Multiple comparisons (LSD) in the plant functional traits among scars (S), deposits (D) and the surrounding vegetated areas (SVA)

Plant functional trait	*t*-value		$Pr(>\|t\|)$
Life span	t_{S-SVA}	0.220	0.827
	t_{S-D}	0.766	0.446
	t_{SVA-D}	0.546	0.586
Growth form	t_{SVA-S}	0.025	0.980
	t_{SVA-D}	0.314	0.754
	t_{S-D}	0.289	0.773
Plant height (maximum height)	t_{S-SVA}	0.230	0.819
	t_{S-D}	0.261	0.795
	t_{SVA-D}	0.031	0.975
Clonality	t_{SVA-S}	0.178	0.859
	t_{SVA-D}	0.519	0.605
	t_{S-D}	0.341	0.734
Seed production	t_{SVA-S}	0.171	0.865
	t_{SVA-D}	0.418	0.677
	t_{S-D}	0.249	0.804
Seed dispersal mode	t_{D-S}	0.241	0.810
	t_{D-SVA}	0.247	0.805
	t_{S-SVA}	0.006	0.995
Seed mass	t_{S-D}	0.118	0.906
	t_{S-SVA}	0.353	0.725
	t_{D-SVA}	0.235	0.815
Seed anchorage	t_{SVA-D}	0.017	0.987
	t_{SVA-S}	0.197	0.844
	t_{D-S}	0.180	0.858
Seed germination rate	t_{SVA-S}	0.027	0.978
	t_{SVA-D}	0.035	0.972
	t_{S-D}	0.008	0.994
Seed first germination	t_{S-SVA}	0.147	0.883
	t_{S-D}	0.183	0.855
	t_{SVA-D}	0.036	0.971
Resprouting capacity	t_{SVA-D}	0.016	0.987
	t_{SVA-S}	0.555	0.580
	t_{D-S}	0.539	0.591

Table S4 Multiple comparisons (LSD) in the soil properties among scars (S), deposits (D) and the surrounding vegetated areas (SVA)

Soil property	*t*-value		$Pr(>\left\|t\right\|)$
Slope angle	$t_{S\text{-}SVA}$	2.188	**0.033**
	$t_{SVA\text{-}D}$	0.408	0.685
	$t_{S\text{-}D}$	2.565	**0.013**
Clay to sand ratio	$t_{S\text{-}D}$	0.472	0.639
	$t_{S\text{-}SVA}$	0.913	0.366
	$t_{D\text{-}SVA}$	0.466	0.643
Bulk density	$t_{S\text{-}D}$	0.158	0.875
	$t_{S\text{-}SVA}$	1.477	0.146
	$t_{D\text{-}SVA}$	1.317	0.194
Available water	$t_{D\text{-}SVA}$	0.075	0.941
	$t_{D\text{-}S}$	0.095	0.924
	$t_{SVA\text{-}S}$	0.021	0.984
Organic matter	$t_{SVA\text{-}D}$	1.306	0.197
	$t_{SVA\text{-}S}$	1.793	0.079
	$t_{D\text{-}S}$	0.662	0.511
Inorganic nitrogen	$t_{SVA\text{-}D}$	0.329	0.744
	$t_{SVA\text{-}S}$	0.438	0.663
	$t_{D\text{-}S}$	0.110	0.913
Available phosphorus	$t_{S\text{-}SVA}$	0.044	0.965
	$t_{S\text{-}D}$	0.177	0.860
	$t_{SVA\text{-}D}$	0.133	0.895
Soil moisture in 0–5 cm layer within the growing season of 2015	$t_{D\text{-}S}$	0.126	0.900
	$t_{D\text{-}SVA}$	0.324	0.747
	$t_{S\text{-}SVA}$	0.201	0.841
Soil moisture in 0–5 cm layer within the growing season of 2016	$t_{D\text{-}S}$	0.254	0.800
	$t_{D\text{-}SVA}$	0.741	0.460
	$t_{S\text{-}SVA}$	0.488	0.626

Table S5 The average values of species density in scars (S), deposits (D) and the surrounding vegetated areas (SVA). The most abundant species in S, D and SVA are emphasized in bold

Species	The average species density (individuals m^{-2})		
	S	D	SVA
Adenophora potaninii Korsh.	0.0017	0.0076	0.0242
Ailanthus altissima (Mill.) Swingle var. *altissima*	0.0044	0.0022	0.0278
Allium chrysanthum Regel	0	0.0010	0.0062
Amorpha fruticosa L.	0	0.0003	0
Ampelopsis delavayana Planch. var. *delavayana*	0	0.0138	0.0433
Anemone vitifolia Buch.-Ham.	0.0049	0.0008	0.0021
Aristolochia contorta Bunge	0	0.0069	0
Armeniaca sibirica (L.) Lam. var. *sibirica*	0	0	0.0044
Artemisia annua L.	0.0042	0.0333	0.1113
Artemisia argyi Levl. et Van. var. *argyi*	0.0184	0.1123	0.1185
Artemisia carvifolia Buch.-Ham. var. *carvifolia*	0	0.0043	0
Artemisia giraldii **Pamp.**	**0.2971**	**0.4508**	**1.2516**
Artemisia gmelinii **Web. ex Stechm.**	**0.1868**	**0.3930**	**1.3930**
Artemisia japonica Thunb. var. *japonica*	0.0272	0.1649	0.1724
Artemisia mongolica (Fisch. ex Bess.) Nakai	0.0413	0.0982	0.2295
Artemisia scoparia **Waldst. et Kit.**	**0.0876**	**0.2318**	**0.3973**
Arundinella anomala Steud.	0.0051	0.0064	0.0410
Asparagus cochinchinensis (Lour.) Merr.	0	0.0003	0.0017
Aster ageratoides Turcz.	0.0274	0.0497	0.0174
Astragalus discolor Bunge ex Maxim.	0.0290	0.0153	0.0353
Astragalus melilotoides Pall. var. *melilotoides*	0.0239	0.0723	0.1565
Astragalus scaberrimus Bunge	0.0029	0.0035	0.0114
Berberis amurensis Rupr.	0.0077	0	0.0133
Bidens parviflora Willd.	0.0137	0.1564	0.0776
Bothriochloa ischaemum **(L.) Keng**	0.0551	0.1403	**0.6179**
Buddleja alternifolia Maxim.	0.0092	0.0133	0.0499
Bupleurum yinchowense Shan et Y. Li	0.0056	0.0242	0.1036
Calamagrostis epigeios **(L.) Roth var.** ***epigeios***	**0.0694**	0.1010	0.0899
Carex lanceolata Boott var. *lanceolata*	0.0359	0.1333	0.1883
Chenopodium glaucum L.	0	0.0043	0
Cirsium setosum **(Willd.) MB.**	0.0481	**0.2668**	0.1470
Cleistogenes caespitosa **Keng**	**0.1288**	**0.2633**	**0.9058**
Cleistogenes hancei Keng	0.0065	0.0066	0.0769
Cleistogenes squarrosa (Trin.) Keng	0.0087	0.0172	0.0200
Clematis aethusifolia Turcz.	0.0013	0	0
Clematis fruticosa Turcz.	0.0010	0.0060	0.0683
Convolvulus arvensis L.	0.0108	0.0558	0.0104
Conyza Canadensis (L.) Cronq.	0	0.0046	0
Cynanchum chinense R. Br.	0.0041	0.0345	0.0146
Cynanchum thesioides (Freyn) K. Schum. var. *thesioides*	0.0176	0.0741	0.0349
Delphinium grandiflorum L.	0	0.0053	0.0067
Dendranthema chanetii **(Levl.) Shih**	**0.1241**	**0.7079**	**2.3788**
Dendranthema indicum **(L.) Des Moul.**	0.0126	**0.6207**	0.1000
Diarthron linifolium Turcz.	0.0011	0.0027	0.0290
Dracocephalum moldavica L.	0.0141	0.0226	0.0913
Erodium stephanianum Willd.	0.0199	0.0317	0.1074

Euphorbia humifusa Willd. ex Schlecht.	0	0.0034	0.0017
Geranium sibiricum L.	0.0320	0.0735	0.0943
Glycyrrhiza uralensis Fisch.	0.0017	0.0138	0.0229
Gueldenstaedtia stenophylla Bunge	0.0034	0.0060	0.0088
***Heteropappus altaicus* (Willd.) Novopokr.**	**0.0701**	0.1146	**0.2875**
Hippophae rhamnoides L.	0	0.0403	0.0179
Hypecoum erectum L.	0	0	0.0028
Incarvillea sinensis Lam. var. *sinensis*	0	0.0270	0.0417
***Ixeridium chinense* (Thunb.) Tzvel.**	**0.0915**	0.0224	0.0463
***Ixeridium sonchifolium* (Maxim.) Shih**	**0.1795**	**0.2295**	**0.3288**
Koeleria cristata* (L.) Pers. var. *cristata	**0.1146**	0.0599	**0.5707**
Lappula myosotis V. Wolf	0	0.0118	0.0067
***Leontopodium leontopodioides* (Willd.) Beauv.**	0.0015	0.0128	**0.3373**
Leonurus sibiricus L.	0	0.0138	0.0033
Lespedeza daurica* (Laxm.) Schindl. var. *daurica	**0.0960**	0.0817	**0.4928**
Lespedeza floribunda Bunge	0.0275	0.1002	0.1819
Lespedeza juncea (L. f.) Pers.	0.0044	0.0150	0.0657
***Leymus secalinus* (Georgi) Tzvel.**	**0.1137**	**0.2518**	**0.4549**
Linum usitatissimum L.	0.0006	0	0.0125
Medicago lupulina L.	0	0.0006	0.0050
Medicago ruthenica (L.) Trautv.	0	0.0073	0.0058
Melica radula Franch.	0.0437	0.0474	0.0507
Melica scabrosa Trin. var. *scabrosa*	0	0.0050	0.0417
Melilotus albus Medic. ex Desr.	0.0006	0	0.0033
Melilotus officinalis (L.) Pall.	0	0.0138	0
Orobanche coerulescens Stephan ex Willd. f. *coerulescens*	0	0	0.0014
Ostryopsis davidiana Decne.	0	0	0.0033
Oxytropis bicolor Bunge var. *bicolor*	0	0	0.0024
***Patrinia heterophylla* Bunge**	**0.1636**	**1.2641**	**3.0651**
Pennisetum centrasiaticum Tzvel. var. *centrasiaticum*	0.0010	0.0637	0.0063
***Periploca sepium* Bunge**	**0.1167**	0.1299	**0.4729**
Peucedanum terebinthaceum (Fisch. ex Trevir.) Ledeb. var. *terebinthaceum*	0.0071	0.0191	0.0515
Phragmites australis* (Cav.) Trin. ex Steud. var. *australis	**0.1079**	**0.3022**	0.2011
Plantago depressa Willd. subsp. *depressa*	0	0.0065	0
***Poa sphondylodes* Trin.**	**0.2416**	**0.4115**	**0.7590**
Polygala tenuifolia Willd.	0.0273	0.0084	0.1187
Potentilla bifurca L. var. *bifurca*	0	0	0.0083
Potentilla saundersiana Royle var. *subpinnata* Hand.-Mazz.	0.0011	0	0.0194
Potentilla tanacetifolia Willd. ex Schlecht.	0.0527	0.0836	0.1623
Pulsatilla chinensis (Bunge) Regel	0.0039	0.0007	0.0048
Pyrus betulifolia Bunge	0	0	0.0021
Rehmannia glutinosa (Gaetn.) Libosch. ex Fisch. et Mey.	0	0.0037	0.0090
Rhamnus erythroxylon Pall.	0.0009	0	0.0073
Robinia pseudoacacia L. var. *pseudoacacia*	0.0101	0.0043	0.0522
Roegneria ciliaris* (Trin.) Nevski var. *ciliaris	**0.0868**	0.1695	0.1974
Rubia cordifolia L.	0	0.0157	0.1242
Rubus parvifolius L. var. *parvifolius*	0.0046	0.0156	0.0500
Salsola collina Pall.	0.0088	0.1568	0.1433
Saussurea japonica (Thunb.) DC.	0.0121	0.1324	0.0757
Scorzonera sinensis Lipsch. et Krasch. ex Lipsch.	0.0015	0	0
Serratula centauroides L.	0.0014	0	0

Setaria viridis **(L.) Beauv. subsp.** ***viridis***	0.0546	**0.5082**	**0.6884**
Sonchus oleraceus **L.**	**0.1081**	**0.3168**	**0.4454**
Sophora davidii (Franch.) Skeels var. *davidii*	0.0048	0.0508	0.2251
Speranskia tuberculata (Bunge) Baill.	0	0.0029	0
Sphaerophysa salsula **(Pall.) DC.**	**0.2271**	0.0924	0.1643
Stipa bungeana **Trin.**	**0.1645**	**0.3503**	**1.0378**
Stipa grandis P. Smirn.	0.0025	0.1027	0.1717
Syringa oblata Lindl. var. *oblata*	0	0	0.0017
Taraxacum mongolicum Hand.-Mazz.	0.0081	0.0170	0.0345
Thalictrum petaloideum L.	0	0	0.0042
Thermopsis lanceolata **R. Br. var.** ***lanceolata***	0.0346	**0.2226**	0.0706
Ulmus pumila L.	0.0018	0.0006	0.0050
Vicia amoena **Fisch. ex DC. var.** ***amoena***	**0.0845**	**0.4915**	**0.4588**
Viola dissecta Ledeb.	0.0183	0.0754	0.1810
Viola philippica Cav.	0.0029	0.0018	0.0170
The total number of species	81	95	101