Plant Ecol (2019) 220:595–603
https://doi.org/10.1007/s11258-019-00938-9

Species turnover differentiates diversity–disturbance relationships between aboveground vegetation and soil seedbank

Yushin Shinoda · **Munemitsu Akasaka**

Received: 26 June 2018 / Accepted: 10 April 2019 / Published online: 27 April 2019

Abstract An understanding of relationships between species diversity and disturbance gradient is important to comprehend the role of disturbances in the structure of plant communities. Although some studies have demonstrated incongruence in diversity–disturbance relationships (hereafter DDRs) between aboveground vegetation and soil seedbank, the process that causes the difference remains unclear. This incongruence between the two DDRs could result in the decrease in the source of recovery of aboveground vegetation following disturbances being overlooked when only aboveground vegetation is surveyed. Here, we verified a process that species turnover across the disturbance gradient causes the incongruence. Based on a vegetation and seedbank survey, we examined DDRs and species turnover of aboveground vegetation and seedbank along disturbance duration (i.e., excluding years of ungulate grazing). The degree of species turnover was considerably greater in aboveground vegetation than in seedbank; thus, the degree of species turnover along a disturbance gradient caused the difference in DDR between aboveground vegetation and seedbank.

Keywords Disturbance–diversity relationships · Ungulate grazing · Intermediate disturbance hypothesis · Soil seedbanks · Aboveground vegetation · Forest ecosystem

Introduction

Disturbances have a major impact on current and future species richness as well as on plant community structure (Lindenmayer et al. 2010; Turner 2010). The effect of disturbance on species richness varies along the disturbance gradient (Connell 1978; Miller et al. 2011). Therefore, understanding diversity–disturbance relationships (hereafter referred to as DDRs) are crucial to comprehend the role of disturbance in species richness (Hall et al. 2012; Yeboah and Chen 2016).

The species richness of seedbanks plays a vital role in determining species richness and stability of aboveground vegetation (Oesterheld and Sala 1990; DiTommaso et al. 2014); hence, it is essential to understand variation in species richness of seedbanks along disturbance gradients. However, previous studies have mainly assessed DDRs by focusing on

---

Communicated by Neal J. Enright.

Y. Shinoda (✉)
United Graduate School of Agricultural Science, Tokyo University of Agriculture and Technology, Fuchu, Tokyo 183-8509, Japan
e-mail: yushin0423@yahoo.co.jp

M. Akasaka
Institute of Agriculture, Tokyo University of Agriculture and Technology, Fuchu, Tokyo 183-8509, Japan

Table 1 Ratio of the number of recruited species to that of baseline species in aboveground vegetation compared with that in seedbanks

	Estimate	SD	*P*
Intermediate			
Intercept	− 1.1	0.41	0.01
Aboveground	1.5	0.76	0.056
Long			
Intercept	− 0.98	0.48	0.04
Aboveground	1.9	0.96	0.049

Estimated coefficients of aboveground > 0 indicate that the ratio of the number of recruited species to that of baseline species was greater in aboveground vegetation than in seedbanks

aboveground vegetation and have rarely assessed DDRs in soil seedbanks (González et al. 2010; Ma et al. 2013). Although limited studies have concurrently examined DDRs in both seedbanks and aboveground vegetation, some have detected incongruence between them (i.e., the pattern of DDRs differed between aboveground vegetation and seedbanks) (Pellissier et al. 2008; Loydi et al. 2012). This incongruence between the two DDRs can result in the decrease of the source of recovery of aboveground vegetation following disturbances being overlooked when only the response of aboveground vegetation against disturbance is surveyed. Therefore, comprehending the incongruence could help the ecosystem management planning before disturbance causes catastrophic damage to seedbank. Despite this detection of incongruence and its plausible consequences, to the best of our knowledge, no studies to date have empirically elucidated the process causing this incongruence between the two DDRs.

Species turnover along disturbance gradients has been deemed as the major determinant of DDRs (Connell 1978; Suzuki et al. 2013). Therefore, species turnover along disturbance gradients could be responsible in causing the incongruence in the two DDRs, although this has not yet been tested. In aboveground vegetation, the major process controlling disturbance-driven turnover is an increase in opportunities for less competitive and disturbance-tolerant species to germinate from seedbanks and become established; this is triggered by the decline of dominant species, which are frequently competitive but disturbance-intolerant (Suzuki et al. 2013). Species recruitment following a disturbance can cause a hump-shaped DDR (with maximum species richness under an intermediate disturbance regime) (Miller et al. 2011; Yeboah and Chen 2016). In contrast, although this issue has been untested, species recruitment following a disturbance could be more limited in seedbanks than in aboveground vegetation for the following reason: species recruitment in aboveground vegetation following a disturbance that increases its species richness would not increase the species richness of the seedbank, when the recruited species have originated from the seedbank. Furthermore, when the recruited species mostly originate from the seedbank, the species richness of seedbanks would consequently decrease over time because of species loss caused by germination and death. In addition, continuous disturbance decreases the number of seeds in seedbank by promoting germination and restricting reproduction. Therefore, the change in the number of species recruited following a disturbance could be integral in causing incongruence in DDRs between aboveground vegetation and seedbanks. In particular, limitations in recruitment in seedbanks can be apparent when seed production and dispersal are restricted by continuous disturbance and/or when seed arrival from outside the system is limited.

Considering this background, the present study aimed to shed light on the process causing incongruence in DDRs between aboveground vegetation and seedbanks. We investigated whether the relationship between plant species richness and disturbance gradient (i.e., disturbance duration) is consistent between aboveground vegetation and seedbanks. In particular, we hypothesized that the number of recruited species along a disturbance gradient differs between aboveground vegetation and seedbanks, which consequently causes incongruence in DDRs between aboveground vegetation and seedbanks. We focused on a forest ecosystem as a model ecosystem exposed to heavy ungulate grazing. Ungulate grazing results in the continuous disturbance of plant reproduction and strongly defines plant species richness and seed reproduction in several regions in the northern hemisphere (Côté et al. 2004; Takatsuki 2009). A clear verification of the process causing incongruence in DDRs between aboveground vegetation and seedbanks is possible when the seedbank is the sole source of recruited species in aboveground vegetation.

Therefore, we selected an island as the study area on which seed dispersal from external ecosystems is considered to be highly limited. The following two hypotheses were tested: (1) the species richness of seedbanks monotonically decreases with increasing disturbance duration, although species richness of aboveground vegetation is maximized at intermediate disturbance duration and (2) species turnover due to the change of disturbance duration in seedbanks is smaller than that in aboveground vegetation.

Materials and methods

Our study area was Nakajima Island (4.84 km^2) situated in the middle of Lake Toya, Hokkaido, Northern Japan (42.5°N, 140.8°E). This island is located at least 3 km away from the mainland. The annual precipitation and mean annual temperature in the region are 518.0 mm and 8.7 °C, respectively. The mean monthly temperature ranges from − 3.8 to 21.7 °C (data obtained from the Date Climatological Observatory of Muroran, located within 30 km of the study area). The snow-free period extends between April and November, whereas the growing season for plants extends mainly between June and October. Most of the island is covered by natural, broad-leaved forests comprising species such as *Acer pictum* Thunb. subsp. *momo* H. Ohashi and *Tilia japonica* Shimonk var. *japonica* (Sukeno and Miyaki 2007). The large ungulate *Cervus nippon yesoensis* Heude (1.5 m in mean withers height) was introduced to the island in 1957–1966 and inhabits the entire island. The understory vegetation experienced heavy and frequent grazing for about 30 years due to abundant ungulates (21–91 individuals/km^2 for about 30 years until 2012 and approximately 12 individuals/km^2 thereafter) (Takeshita et al. 2015). During the period of peak ungulate density, ungulates foraged litter as well as some unpalatable plant species (Takahashi and Kaji 2001). Several exclosures (approximately 10 × 10 m in size) were installed on the island in 1984 (before the rapid increase in ungulate density; hereafter referred to as 1984 exclosures); moreover, exclosures (approximately 30 × 30 m) were installed in 2004 (at the peak of ungulate density; 2004 exclosures). In the present study, we set up two sites, with each site comprising one exclosure installed in 1984, one exclosure installed in 2004, and one control plot (i.e., no exclosure installed). These exclosures and control plot were located in close proximity to each other (within < 10 m). Each exclosure and control plot was divided into four square subplots, and a 1 × 1-m quadrat was placed at the center of each subplot (24 quadrats in total).

Vegetation survey

A vegetation survey was conducted during July 2015. All vascular plant species were identified and recorded with a height of < 2 m in each quadrat. The upper limit of the plant height was set to 2 m according to the maximum reach for ungulate grazing (Miyashita et al. 2007). We did not survey plants higher than 2 m because we focused on the effects of deer grazing on understory vegetation. In addition, we assumed that plants higher than 2 m do not appear to bias the effect on understory vegetation among each treatment (exclosures installed in 1984, 2004 and controls) because the levels of canopy openness at a height of 2 m were similar in each plot (mean of canopy openness in each plot = 28.6%, variance = 8.92).

Soil sampling

Five soil cores (5.0 cm in diameter and 5.1 cm in height) were randomly sampled from the surface layer of each quadrat during July 2015, after the peak of germination for most plant species in the study area. Soil samples were protected from sunlight after collection and transferred to the laboratory.

Germination experiment

Soil samples were enclosed in plastic bags and stored in dark, cold conditions (5 °C) for 3 months. Following the work of Milberg (1995), the germination experiment was initiated during October 2015 using half of each sample (50 mL) after thorough mixing. The soil was stored as thin layers (≤ 1 cm) on 2-cm-thick vermiculite in plastic packs (115 × 85 × 45 mm) containing several holes in the bottom. The packs were placed in a greenhouse under a light/dark cycle of 12/12 h. The temperature during the light cycle was set to 25 °C, which was the mean of the highest daily temperatures during August in the study area, whereas the temperature during the dark cycle was set to 13 °C, which was the mean of the lowest daily temperatures during June in the study area. The soil was constantly kept moist. The packs were rearranged every 2 weeks to avoid variation in the light conditions. Emerged seedlings were removed following identification. In cases wherein the seedlings were too small to identify, plant growth was maintained for an additional 2 weeks. The experiment was continued until no further germination had occurred for 2 weeks (the experiment was continued for 3 months).

Statistical analysis

Changes in the probability of occurrence along disturbance duration gradient

A generalized linear mixed model was developed to examine the effects of disturbance duration (due to ungulate grazing) on the probability of occurrence of plant species in aboveground vegetation and seedbanks. The presence/absence of plant species in each quadrat was used as a response variable, and disturbance duration, appearance location (aboveground or seedbanks), and their interaction were used as explanatory variables. Using the presence/absence of plant species as a response variable, the effects of disturbance duration on the occurrence of plants could be analyzed accounting for the character of respective species (note that the sum of the probability of occurrence of all species observed is equivalent to the expected species richness). The disturbance duration was used as a categorical variable by setting the following categories: short (exclosures installed in 1984 and thus free from disturbance since 1984), intermediate (exclosures installed in 2004 and thus free from disturbance since 2004), and long (control plots, no interruption of disturbance). Site and species identifications were included as random effects in the model. A logit link function and a binomial error distribution were used.

Change in the ratio of the number of recruited species to that of baseline species with increasing disturbance duration

In the present study, "baseline species" were defined as species found in 1984 exclosures, and "recruited species" were defined as species not found in 1984 exclosures but found in 2004 exclosures or in control plots. To clarify whether the degree of species turnover differed between aboveground vegetation and seedbanks, the ratio of the number of recruited species to that of baseline species between aboveground vegetation and seedbanks was compared for each disturbance duration (intermediate and long). To directly assess the effect of the number of recruited species on total species richness, an approach focusing on the ratio of the number of recruited species to that of baseline species was used instead of ordination analysis or similarity/dissimilarity measures. The following three-step analysis was conducted for the two disturbance durations (intermediate and long). First, plant species observed in aboveground vegetation and seedbanks in association with a particular disturbance duration were listed, following which the lists were combined without removing redundant species (i.e., species appearing in both lists). Information on the observed location (aboveground or seedbanks) of each species in the merged list was retained. Second, respective species were classified into each emergence pattern (baseline species or recruited species). Finally, the generalized linear model was developed, in which the emergence pattern [baseline (0) or recruited species (1)] of respective species is explained by their observed location [aboveground (1) or seedbanks (0)]. A logit link function and a binomial error distribution were used. In cases wherein the coefficient of the explanatory variable was significantly > 0, it indicated that the number of recruited species was significantly greater for aboveground vegetation than for seedbanks. All of the above analyses were performed using the statistical software package R3.4.1 (R Core Team 2014). The generalized linear mixed model and parameter estimation were developed using the lme4 package.

Results

Overall, 23 and 47 species were recorded in the germination experiment and in the plant survey, respectively (Appendix 1). We recorded 23, 31, and 22 species in aboveground vegetation and 17, 10, and 6 species in seedbanks for the short, intermediate, and long disturbance durations, respectively (Fig. 1).

The probability of occurrence with increasing disturbance duration showed different patterns between aboveground vegetation and seedbanks

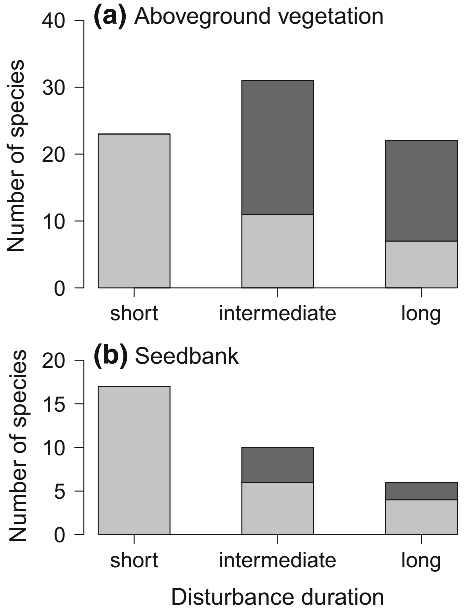

Fig. 1 Species richness of baseline species and that of recruited species in aboveground vegetation and seedbanks for each disturbance duration. Disturbance duration (short, intermediate, long) is compatible with the duration because deer-proof fences were installed (long, short, not installed). Light gray and dark gray bars indicate the species richness of baseline and recruited species, respectively. The ratio of the number of recruited species to that of baseline species was significantly greater in aboveground vegetation than in seedbank for the quadrats with long disturbance duration ($p < 0.05$) (Table 1)

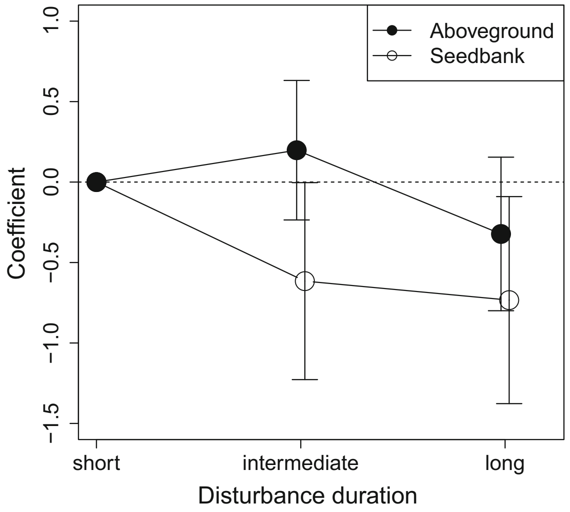

Fig. 2 Coefficients of the probability of occurrence of plant species in aboveground vegetation and seedbanks with increasing disturbance duration. The points indicate the mean of the probability of occurrence, and the bars represent the 95% confidence interval

(Fig. 2). In aboveground vegetation, the probability of occurrence exhibited a hump-shaped pattern with increasing disturbance duration. However, in seedbanks, the probability of occurrence showed a significant monotonic decrease with increasing disturbance duration (Fig. 2).

The degree of species turnover was greater in aboveground vegetation than in seedbanks (Fig. 1). The number of baseline species tended to decrease with increasing disturbance duration in both aboveground vegetation and seedbanks (Fig. 1). However, the number of recruited species was greater in aboveground vegetation than in seedbanks. The number of recruited species was significantly different for the quadrats with long disturbance duration but was marginally different for those with intermediate disturbance duration (Table 1).

Discussion

In the present study, we showed incongruence in DDRs between aboveground vegetation and seedbanks, utilizing long-term experiment settings that excluded ungulate grazing. To the best of our knowledge, this is the first study to explicitly demonstrate that the change in the number of recruited species with increasing disturbance duration is the main cause of incongruence between the two DDRs. Our findings suggest that the number of recruited species rather than that of baseline species is responsible for causing incongruence in DDRs between aboveground vegetation and seedbanks. Consistent with our results, incongruence in DDRs between aboveground vegetation and seedbanks has mostly been reported in studies that focused on intense ungulate grazing (Pellissier et al. 2008; Ma et al. 2010, 2013; Loydi et al. 2012), a pressure-type disturbance (sensu Resilience Alliance 2010; Sasaki et al. 2015) that could limit seed recruitment for a long period (Côté et al. 2004; Sasaki et al. 2015). However, congruence in DDRs has frequently been reported in studies that focused on pulse-type disturbances (e.g., fire, plowing, and wind storm) (Levassor et al. 1990; Wang et al. 2015; Heydari et al. 2017). These pulse-type disturbances do not seem to reduce the number of species recruited following a disturbance (i.e., recruited species) due to limited seed recruitment because these disturbances are unlikely to inhibit plant reproduction for a long period. Therefore, limitations in seed recruitment can determine the pattern of DDR. Although this has not been indicated in previous studies, we suggest that focusing on the change in the number of species recruited following a disturbance along a disturbance gradient can enhance our understanding of the conditions that cause incongruence in the two DDRs and of the roles of disturbance in species richness.

Changes in plant trait composition in seedbanks have been well investigated as a factor that determines DDRs in seedbanks (Pellissier et al. 2008; Loydi et al. 2012; Pakeman and Eastwood 2013). In particular, the number of plant species that can endure disturbances (e.g., through longevity, large seed size, or a large number of seeds) has been focused upon as a factor shaping DDRs in seedbanks (Ma et al. 2013; Pakeman and Eastwood 2013). In addition, our study revealed that the number of plant species recruited following a disturbance could be an important factor shaping DDRs, although our data may be insufficient to completely generalize our hypothesis owing to a lack of additional exclosures suitable for our design and the fact that this work was conducted in a single forest ecosystem. Further studies are required for generalizing the process by which the species richness of recruited species determines the pattern of DDRs.

In conclusion, we verified that limited recruitment in seedbank causes the incongruent DDRs between aboveground vegetation and seedbank through decreasing species turnover in seedbank. The pattern of DDRs in seedbanks showed a decrease in the species richness of seedbanks along the disturbance gradient, whereas that in aboveground vegetation demonstrated a unimodal pattern. This incongruence in these patterns indicates that the future decrease in the important source of recovery of aboveground vegetation cannot be characterized when only aboveground vegetation is monitored or surveyed. In the future, additional surveys on DDRs in seedbanks with a focus on species turnover are required to help both the understanding of the conditions causing incongruence in DDRs and ecosystem management planning before disturbance causes catastrophic damage to seedbank.

Acknowledgements We thank F. Toyama, Y. Ichitani, K. Ando, and K. Suzuki for their help with the field survey and germination experiment. We[m1] are grateful K. Kaji and M. Miyaki for installing deer proof fences in study area in 1984's and 2004. We also thank the staff of Toya Lake Station of Hokkaido University for facilitating comfortable stay and C. Egawa, M. Suzuki, and T. Amano for their generous guidance. We thank Hokkaido Regional Forest Office for the approval of survey in the national forest and park ranger office in Toya Lake and Y. Nakayama for the approval of soil sampling.

Funding This study was partly supported by the Japan Society for the Promotion of Science (no. 16H02555).

Appendix 1

Appendix 1 A list of plant species in seedbank and aboveground

Scientific name	Presence (1) or absence (0)		
	Short	Intermediate	Long
(a) Aboveground vegetation			
Acer buergerianum Miq.	0	1	0
Acer pictum Thunb.	0	1	0
Actinidia arguta (Siebold et Zucc.) Planch. ex Miq. var. *arguta*	0	1	1
Actinidia polygama (Siebold et Zucc.) Planch. ex Maxim.	1	0	0
Aralia elata (Miq.) Seem.	0	1	0
Arisaema japonicum Blume	1	1	1
Cardamine leucantha (Tausch) O. E. Schulz var. *leucantha*	1	0	0
Cayratia japonica (Thunb.) Ganep.	1	0	0
Cephalotaxus harringtonia (Knight ex Forbes) K.Koch var. *nana* (Nakai) Rehder	1	1	0
Cercidiphyllum japonicum Siebold et Zucc. ex Hoffm. et Schult.	0	1	0

Appendix 1 continued

Scientific name	Presence (1) or absence (0)		
	Short	Intermediate	Long
Chloranthus japonicus Siebold	0	1	1
Chloranthus serratus (Thunb.) Roem. et Schult.	0	1	1
Cimicifuga simplex (DC.) Wormsk. ex Turcz.	1	0	0
Clerodendrum trichotomum Thunb. var. *trichotomum*	0	1	1
Codonopsis lanceolata (Siebold et Zucc.) Trautv. var. *lanceolata*	0	1	0
Cornus controversa Hemsl. ex Prain var. *controversa*	1	1	0
Cynanchum caudatum (Miq.) Maxim. var. *caudatum*	0	1	1
Dryopteris crassirhizoma Nakai	1	0	0
Elatostema involucratum Franch. et Sav.	0	1	0
Elsholtzia ciliata (Thunb.) Hyl.	0	0	1
Fraxinus mandshurica Rupr.	0	1	1
Galium japonicum Makino	0	1	0
Galium trifloriforme Kom.	1	1	1
Ixeridium dentatum (Thunb.) Tzvelev subsp. *dentatum*	1	1	1
Kalopanax septemlobus (Thunb.) Koidz. var. *septemlobus*	0	1	1
Lilium medeoloides A.Gray var. *medeolodes*	1	0	0
Maackia amurensis Rupr. et Maxim.	0	1	1
Morus australis Poir.	1	1	0
Ophiopogon japonicus (Thunb.) Ker Gawl. var. *japonicus*	0	0	1
Orchidaceae sp.	1	0	0
Ostrya japonica Sarg.	1	1	0
Pachysandra terminalis Siebold et Zucc.	1	1	1
Padus ssiori (F. Schmidt) C. K. Schneid.	0	1	0
Phellodendron amurense Rupr. var. *amurense*	0	1	1
Poa annua L. var. *annua*	0	0	1
Pteridium aquilinum (L.) Kuhn subsp. *japonicum* (Nakai) Á. et D.Löve	0	0	1
Pterocarya rhoifolia Siebold et Zucc.	1	0	0
Quercus crispula Blume	1	0	0
Sasa palmata (Lat.-Marl. ex Burb.) E.G.Camus var. *palmata*	1	0	0
Senecio cannabifolius Less.	0	1	1
Styrax obassia Siebold et Zucc.	1	1	1
Tilia japonica (Miq.) Simonk. var. *japonica*	1	1	0
Toxicodendron radicans Greene subsp. *orientale*	0	1	0
Toxicodendron trichocarpum (Miq.) Kuntze	1	0	1
Urtica thunbergiana Siebold et Zucc.	1	1	1
Viola grypoceras A.Gray var. *grypoceras*	0	1	1
Zanthoxylum piperitum (L.) DC.	1	0	0
(b) Seedbank			
Ampelopsis glandulosa (Wall.) Momiy. var. *heterophylla* (Thunb.) Momiy.	1	0	0
Asteraceae sp.	1	1	1
Cercidiphyllum japonicum Siebold et Zucc. ex Hoffm. et Schult.	1	0	0
Conyza canadensis (L.) Cronquist	1	0	0
Cynanchum caudatum (Miq.) Maxim. var. *caudatum*	0	1	0

Appendix 1 continued

Scientific name	Presence (1) or absence (0)		
	Short	Intermediate	Long
Galium trachyspermum A.Gray var. *trachyspermum*	1	0	0
Hydrangea petiolaris Siebold et Zucc.	1	1	0
Hydrocotyle maritima Honda	0	0	1
Mazus pumilus (Burm. f.) Steenis	1	0	0
Mosla scabra (Thunb.) C.Y.Wu et H.W.Li	0	1	0
Ostrya japonica Sarg.	1	1	1
Pilea pumila (L.) A. Gray	1	1	1
Poa annua L. var. *annua*	0	1	0
Potentilla fragarioides L. var. *major* Maxim.	1	1	0
Sagina japonica (Sw.) Ohwi	1	1	1
Sasa palmata (Lat.-Marl. ex Burb.) E.G.Camus var. *palmata*	1	0	0
Stellaria neglecta Weihe	1	0	0
Stellaria uliginosa Murray var. *undulata* (Thunb.) Fenzl	0	0	1
Urtica thunbergiana Siebold et Zucc.	1	0	0
Veronica arvensis L.	1	0	0
Violaceae sp.	0	1	0
Unidentified-1	1	0	0
Unidentified-2	1	0	0

This list shows the presence or absence of plant species for each disturbance duration

References

Connell JH (1978) Diversity in tropical rain forests and coral reefs. Science 199:1302–1310

Côté SD, Rooney TP, Tremblay J-P, Dussault C, Waller DM (2004) Ecological impacts of deer overabundance. Annu Rev Ecol Evol Syst 35:113–147

DiTommaso A, Morris SH, Parker JD, Cone CL, Agrawal AA (2014) Deer browsing delays succession by altering aboveground vegetation and belowground seed banks. PloS ONE 9:e91155

González VT, Bråthen KA, Ravolainen VT, Iversen M, Hagen SB (2010) Large-scale grazing history effects on Arctic-alpine germinable seed banks. Plant Ecol 207:321–331

Hall AR, Miller AD, Leggett HC, Roxburgh SH, Buckling A, Shea K (2012) Diversity-disturbance relationships: frequency and intensity interact. Biol Lett 8:768–771

Heydari M, Omidipour R, Abedi M, Baskin C (2017) Effects of fire disturbance on alpha and beta diversity and on beta diversity components of soil seed banks and aboveground vegetation. Plant Ecol Evol 150:247–256

Levassor C, Ortega M, Peco B (1990) Seed bank dynamics of Mediterranean pastures subjected to mechanical disturbance. J Veg Sci 1:339–344

Lindenmayer DB, Likens GE, Krebs CJ, Hobbs RJ (2010) Improved probability of detection of ecological “surprises”. Proc Natl Acad Sci 107:21957–21962

Loydi A, Zalba SM, Distel RA (2012) Viable seed banks under grazing and exclosure conditions in montane mesic grasslands of Argentina. Acta Oecol 43:8–15

Ma M, Zhou X, Du G (2010) Role of soil seed bank along a disturbance gradient in an alpine meadow on the Tibet plateau. Flora 205:128–134

Ma M, Zhou X, Du G (2013) Effects of disturbance intensity on seasonal dynamics of alpine meadow soil seed banks on the Tibetan Plateau. Plant Soil 369:283–295

Milberg P (1995) Soil seed bank after eighteen years of succession from grassland to forest. Oikos 72:3–13

Miller AD, Roxburgh SH, Shea K (2011) How frequency and intensity shape diversity-disturbance relationships. Proc Natl Acad Sci 108:5643–5648

Miyashita T, Suzuki M, Ando D, Fujita G, Ochiai K, Asada M (2007) Forest edge creates small-scale variation in reproductive rate of sika deer. Population Ecol 50:111–120

Oesterheld M, Sala OE (1990) Effects of grazing on seedling establishment: the role of seed and safe site availability. J Veg Sci 1:353–358

Pakeman RJ, Eastwood A (2013) Shifts in functional traits and functional diversity between vegetation and seed bank. J Veg Sci 24:865–876

Pellissier V, Rozé F, Aguejdad R, Quénol H, Clergeau P (2008) Relationships between soil seed bank, vegetation and soil fertility along an urbanisation gradient. Appl Veg Sci 11:325–334

R Core Team (2014) R: A Language and Environment for Statistical Computing

Resilience Alliance. 2010. Assessing resilience in social-ecological systems: Workbook for practitioners. *Resilience Alliance*.

Sasaki T, Furukawa T, Iwasaki Y, Seto M, Mori AS (2015) Perspectives for ecosystem management based on ecosystem resilience and ecological thresholds against multiple and stochastic disturbances. Ecol Indic 57:395–408

Sukeno M, Miyaki M (2007) Impacts of an excessive sika deer population on vascular flora on Nakanoshima Islands, Toya Lake, Hokkaido, Japan. Wildl Conserv Japan 11:43–66

Suzuki M, Miyashita T, Kabaya H, Ochiai K, Asada M, Kikvidze Z (2013) Deer herbivory as an important driver of divergence of ground vegetation communities in temperate forests. Oikos 122:104–110

Takahashi H, Kaji K (2001) Fallen leaves and unpalatable plants as alternative foods for sika deer under food limitation. Ecol Res 16:257–262

Takatsuki S (2009) Effects of sika deer on vegetation in Japan: a review. Biol Conserv 142:1922–1929

Takeshita K, Ishizaki M, Mitsuya R, Takahashi H, Yoshida T, Igota H, Ikeda T, Kubo MO, Kaji K (2015) Temporal changes in molar wear rate of a sika deer population under density-dependent food limitation. J Zool 297:139–145

Turner MG (2010) Disturbance and landscape dynamics in a changing world 1. Ecology 91:2833–2849

Wang YC, Ooi MKJ, Ren GH, Jiang DM, Musa A, Miao RH, Li XH, Zhou Q Lai, Tang J, Lin JX (2015) Species shifts in above-ground vegetation and the soil seed bank in the inter-dune lowlands of an active dune field in Inner Mongolia, China. Basic Appl Ecol 16:490–499

Yeboah D, Chen HYH (2016) Diversity–disturbance relationship in forest landscapes. Landsc Ecol 31:981–987