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Landslides, Alien Species, and the Diversity of a Hawaiian Montane Mesic Ecosystem[1]

Carla Restrepo[2] **and Peter Vitousek**

Department of Biological Sciences, Stanford University, Stanford, California 94305-5020, U.S.A.

ABSTRACT

In the Ninole ridges of Hawai'i, we evaluated changes in plant species diversity and composition and the effect of alien species on the growth and recruitment of native species after disturbance by landsliding. We chose nine landslides representing three age categories (young, 4–17 yr; intermediate, 18–42 yr; and old, *ca* 130 yr) plus three undisturbed forest sites (325–525 yr) to sample and manipulate the vegetation; the undisturbed forest developed on tephra-derived soils underlain by basalt. The ordination of sites and species using detrended correspondence analysis (DCA) showed that species establishing on landslides were different than those found in the undisturbed forest; moreover, a large fraction of the species establishing on young landslides were represented by aliens, mostly grasses and orchids. The manipulation of alien species (clipping of aboveground parts and removal of above- and belowground parts, including soil) on young landslides (<17 yr) significantly affected seedling growth of the native tree species *Metrosideros polymorpha* and the recruitment of native species. In addition, the manipulation of grasses and orchids favored the recruitment of a second group of alien species that were uncommon in, or absent from, our study sites. The removal of tephra-derived soils by landslides, in combination with an increased presence of alien species, may greatly alter successional trajectories in the Ninole ridges of Hawai'i.

RESUMEN

En la sierra Ninole de Hawai'i evaluamos cambios en la diversidad y composición de la vegetación y el efecto de plantas exóticas sobre el crecimiento y reclutamiento de especies nativas resultantes de los deslizamientos de tierra. Escogimos nueve deslizamientos clasificados de acuerdo a tres categorías (jóvenes, 4–17 años; intermedios, 18–42 años; viejos, *ca* 130 años) y tres sitios de bosque no perturbado (325–525 años) para muestrear y manipular la vegetación; los bosques no perturbados se encontraron en suelos derivados de cenizas volcánicas depositados sobre basaltos. La ordenación de los sitios y especies utilizando el método de análisis de corespondencia ajustado (ACA) mostró que las especies establecidas en los deslizamientos difieren de aquellas establecidas en el bosque no perturbado; más aún, una gran proporción de las especies establecidas en los deslizamientos jóvenes correspondieron a especies exóticas, en su mayoría gramíneas y orquídeas. La manipulación de especies exóticas (el corte de estructuras aéreas y la remoción de estructuras áreas y subáreas incluyendo el suelo) en los deslizamientos jóvenes (<17 años) afectaron de manera significativa el crecimiento de plántulas de la especie arbórea nativa *Metrosideros polymorpha* y el reclutamiento de otras especies nativas. Adicionalmente, la manipulación de gramíneas y orquídeas favoreció el reclutamiento de un segundo grupo de especies exóticas poco comunes o que no habían sido registradas en nuestros sitios de estudio. La remoción de suelos derivados de cenizas volcánicas que resultan de los deslizamientos de tierra, en combinación con la presencia de especies exóticas, tiene el potencial de alterar de manera significativa las trayectorias de sucesión vegetal en la sierra Ninole de Hawai'i.

Key words: alien species; disturbance; diversity; landslides; montane tropical forest; succession; Hawai'i.

PATTERNS OF SPECIES DIVERSITY IN WET, TROPICAL MONTANE ECOSYSTEMS may be strongly influenced by landslides (Stebbins 1965; Gentry 1982,1986, 1992; Luteyn 1989; Henderson *et al.* 1991). Landslides, unlike other large-scale disturbances, strongly affect soil characteristics; the areas from which vegetation and soil are removed are colonized by a narrow array of species that can thrive under the harsh and ephemeral conditions found in the recently disturbed substrates (Veblen 1979, Guariguata 1990, Dalling 1994, Myster & Walker 1997).

In spite of their potentially important role in structuring tropical montane ecosystems, landslides have remained underrepresented in studies aimed at understanding the factors influencing biological diversity (*cf.* Walker *et al.* 1996). This is particularly true for the islands of Hawaii, where most work has concentrated on the shallow slopes of the remaining undissected surfaces of the volcanoes

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[2] Current address: Department of Biology, University of Puerto Rico, P.O. Box 23360, San Juan, Puerto Rico 00931-3360, U.S.A.

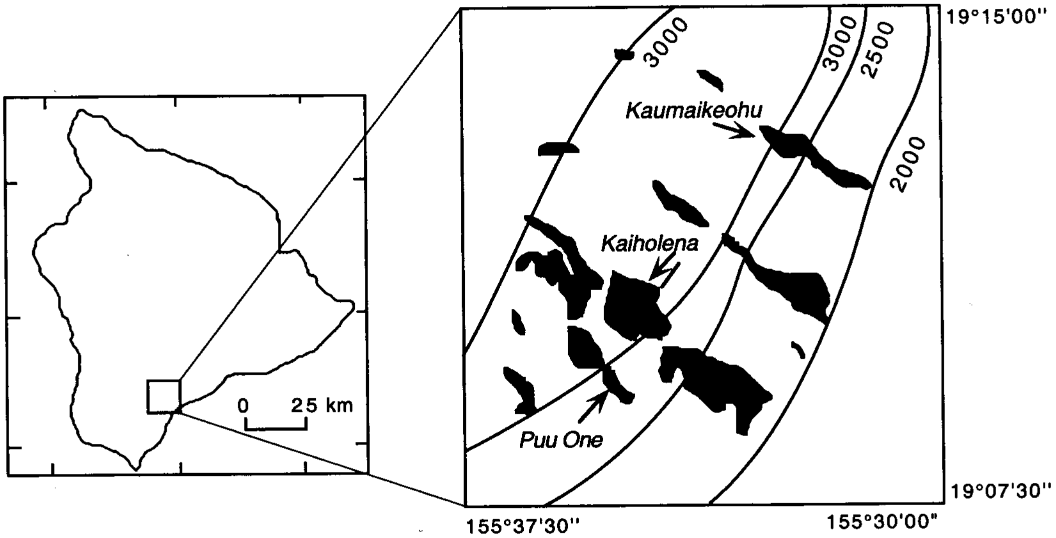

FIGURE 1. Location of the Ninole ridges on the Island of Hawai'i. The hills or ridges that comprise the system are in black. Landslides were sampled at three of these ridges: Kaiholena, Puu One, and Kamaikeahu. Lines are mm isohyets of rainfall; modified after Wolfe and Morris (1996).

(Kitayama & Mueller-Dombois 1995, Kitayama *et al.* 1995, Raich *et al.* 1997, Vitousek & Farrington 1997). Steep slopes, however, become the dominant feature of Hawaiian landscapes as the volcanoes age (Moore & Mark 1992) and landsliding represents the most important denudation process affecting these slopes (Wentworth 1943, Scott & Street 1976, Li 1988, Hill *et al.* 1997).

The study of landslides and their influence on ecosystems may have a further consequence. Landslides may favor the spread of weeds and alien species through mechanisms that are not well understood (Lundgren 1978, Miles *et al.* 1984, Willmott 1984, Meyer 1996). First, landslides, by breaking up the soil profile, disrupt the seed bank and expose unfertile soils (Willmott 1984). Second, landslides and alien plant species with shallow root systems may act synergistically to increase the frequency of landsliding and thus, the further spread of alien plants (Meyer 1996). The pervasiveness of biological invasions in the Hawaiian islands, greatly facilitated by disturbance (Hughes *et al.* 1991, Loope & Giambelluca 1998, Mack & D'Antonio 1998), and the fact that landslides can occur without human intervention, suggest that landslides may exacerbate the threat of invasion by alien plant species in montane mesic to wet ecosystems developing in the remote, dissected surfaces of the islands. In this paper, we ask (1) how landsliding affects species diversity of a Hawaiian montane mesic ecosystem and (2) how alien plant species influence colonization and establishment of native species on landslides.

STUDY SITE

We conducted this study in the Ninole ridges, Kau District, southeastern portion of the island of Hawai'i (19°10′14″N and 155°34′35″W; Fig. 1). The Ninole comprise several hills or ridges that represent remnants of the second oldest volcanic structure of the island (0.1–0.2 Ma, possibly as old as 0.3 Ma; Lipman *et al.* 1990, Wolfe & Morris 1996); together with the extinct Kohala volcano, the Ninole ridges exhibit the steepest topography of the island of Hawai'i (Hitchcock 1906, Stearns & Macdonald 1946, Moore & Mark 1992). In part because of their relative remoteness and in part because of the high rainfall, most of the ridges have been little influenced by human activities. Currently, many of these ridges are within the Kau Forest Reserve.

Overall, the altitude of these ridges ranges from 480–1,116 m, and that of our sampling sites at Puu One, Kaiholena, and Kaumaikeohu ranged from 752–900 m. Based on a 5.8×10^{-3}°C/m lapse temperature rate, our sites have a mean annual temperature of 20°C (Atlas of Hawaii 1983). The nearest active climatological station is located between Puu One and Makaalia and shows a total annual average rainfall of 4095 ± 1099 mm (Hilea Gulch, 900 m; DNLR 1983). A climatological station that operated at the base of Kaiholena between 1964 and 1972 yielded a total annual average rainfall of 2954 ± 586 mm (Field 750, 636 m; DNLR 1983). According to these data, our sites can be classified as subtropical wet forest (Holdridge 1967) or montane mesic forest (Loope 2000). Mesic forests in the Kau Forest Reserve, as elsewhere in the islands of Hawaii, have a closed to open canopy dominated by the native tree *Metrosideros polymorpha* and the tree fern *Cibotium* sp. (Jacobi 1978).

Undisturbed soils in the Ninole ridges are derived from volcanic tephra underlain by basalt. The soils are shallow (35 cm in depth until reaching the hard basalt) and have been classified as hydrous, perrihydritic, isothermic Lithic Hydrudands (R. Gavenda, pers. comm.). Soils from landslides are shallower and represent a mixture of organic matter and variable amounts of soil from different horizons.

METHODS

At Puu One, Kaiholena, and Kaumaikeohu, we identified landslides of various ages using aerial photographs (years 1953, 1954, 1965, 1978, and 1992), dating charcoal remains, and examining historical earthquake records (Restrepo & Vitousek, pers. obs.). We distinguished three landslide age categories (young, 4–17 yr; intermediate, 18–42 yr; and old, *ca* 130 yr) plus the undisturbed forest (325–525 yr) and located three replicates for each (Fig. 1). Landslide width and length ranged from 15 to 40 m and 100 to 150 m, respectively. In the upper part of each landslide we delimited a 20 × 15 m plot perpendicular to the contour lines, with the 20 m axes adjacent to the landslide edges. In the undisturbed forest sites, the plots were placed at random but always with the longest axis perpendicular to the contour lines. The plots were further subdivided into 12 5 × 5 m subplots, 8 located at the edge and 4 at the center of the landslides; 2 edge and 2 center subplots were selected at random per plot to sample the vegetation. We stratified our sampling procedure to take into account variation in species composition from the edge to the center of the landslides (Walker & Neris 1993, Myster & Fernández 1995).

PLANT DIVERSITY AND COMPOSITION.—Sampling of the vegetation took place between August 1996 and August 1997. Trees and shrubs with diameter at breast height (dbh) ≥2.8 cm were sampled in each of the four 5 × 5 m subplots. Trees and shrubs with dbh <2.8 cm, basically saplings, and herbaceous plants (forbs, grasses, sedges, orchids, vines, and rhizomatous plants) were subsampled in each of four 1.5 × 1.5 m quadrats within the 5 × 5 m subplots. We counted, identified to species, and measured the diameters (stems ≥2.8 and <2.8 cm, 1.3 and 0.2 m above ground, respectively) of all individuals. For herbaceous plants, we estimated percent cover as the proportion of ground covered by each species within the quadrats.

ALIEN PLANT SPECIES AND ESTABLISHMENT ON LANDSLIDES.—In young landslides, almost all of the herbaceous plant cover consisted of alien species, mainly grasses and orchids (mean percent cover of alien and native species was 89 and 31%, respectively). These plants not only create a dense cover that affects light conditions near the ground (Hughes & Vitousek 1993, D'Antonio *et al.* 1998), but also develop a thick mat of live and dead roots (C. Restrepo, pers. obs.) that can alter soil conditions. We designed an experiment to evaluate whether the dense areal cover or root mats of these alien plants influenced the recruitment and growth of native species colonizing young landslides. Three of the four 1.5 × 1.5 m quadrats into which the 5 × 5 m subplots were divided were assigned to one of three treatments: (B) removal of all vegetation and soil to expose the basalt; (CL) removal of all the aerial parts of the vegetation without disturbing the soil by clipping plants, and (C) control. The experiments were established in February 1997 on the three young landslides and followed until February 1998; in August 1997, we again clipped grasses and orchids that were resprouting or spreading from the sides.

To evaluate the role of alien plant species on the recruitment of native plant species, we identified and counted all new seedlings that had established in the year after initiating the experiment. New seedlings were nearly absent from the control plots after the experiment was terminated; thus, our analyses were based on the clipped and bare rock quadrats only. To evaluate the influence of alien plant species on the growth of native species, we transplanted seedlings of *M. polymorpha* into the experimental quadrats of two young landslides at Kaiholena. *Metrosideros polymorpha* is the single most abundant tree in Hawaiian mesic and wet forests, including our study sites. Seedlings averaging 4 cm in height that were growing on logs or rocks in nearby undisturbed forests were collected

TABLE 1. *Plant species richness and diversity in the Ninole ridges.*

	No. native	No. alien	Total	Diversity[1]
Young	15	13	28	7.4
Intermediate	17	18	35	9.8
Old	18	11	29	8.1
Undisturbed	19	4	23	5.7

[1] Based on the Shannon diversity index. We used the number of subplots in which species were present as an estimate of their abundance.

and transplanted into the experimental quadrats with a soil bedding made with mosses and soil from the landslides. In total we transplanted 144 seedlings (6 seedlings, 3 quadrats, 4 subplots, 2 landslides), marked them with yellow paint 1 cm above the root zone, and measured their height up to the terminal bud. We recorded the increment in height from the yellow mark in August 1997 and February 1998. Seedling survival was estimated as the number of seedlings that were alive at the end of the experiment.

DATA ANALYSIS.—Patterns in species composition and abundance associated with the formation of landslides were evaluated using a detrended correspondence analysis (DCA). This method allows the simultaneous ordination of samples and species along the main axes of the DCA; samples are separated along the axes based on variation in species composition and abundance. Herbaceous plants were analyzed separately from non-herbaceous plants because we used different variables to estimate their abundance (percent plant cover versus basal area, respectively). Analyses were carried out using CANOCO version 3.1 (ter Braak 1988).

RESULTS

PLANT DIVERSITY AND COMPOSITION.—We recorded a total of 46 plant species, 18 of them alien to the Hawaiian islands (Appendix). Total number of species, or species richness, did not vary among the three landslide-age categories and the undisturbed forest. Yet species diversity, as described by the Shannon index, was highest for the intermediate landslides and lowest for the undisturbed forest (Table 1). Discriminating between native and alien plant species showed that the latter made a substantial contribution to the above results (goodness of fit test: $G = 7.9$, df = 3, $P = 0.05$; Table 1). More alien plant species and more native plant species than expected were recorded in the intermediate and undisturbed forests, respectively.

Plant species clearly segregated among the three landslide classes and the undisturbed forest, suggesting that abiotic and biotic conditions differ among the four habitats. The DCA based on the abundance of herbs separated young and intermediate landslides from old landslides and undisturbed forest along the first axis of the ordination and young from intermediate landslides along the second axis (Fig. 2). We observed an increased abundance of the aliens *Andropogon virginicus, Schizachyrium condensatum* (grasses), and *Arundina graminifolia* (orchid) and the natives *Machaerina angustifolia* (sedge) and *Odontosoria chinensis* (fern) in young landslides. In the landslides of intermediate age, the aliens *Paspalum conjugatum* (grass), *Ageratina riparia, Cuphea carthagenensis* (rhizomatous forbs), *Rubus argutus* (prostrated shrub), and *Nephrolepis multiflora* (fern), and small individuals of the native tree fern, *Cibotium glaucum* (Fig. 2) increased in abundance. Lastly, in the old landslides and the undisturbed forest the natives *Isachne distichophylla* (grass), *Dicranopteris linearis* (fern), *Hedyotis centranthoides* (vine), and *Smilax melastomifolia* (vine) increased in abundance. All three landslide-age categories and the undisturbed forest shared small individuals of the native tree fern *Sadleria pallida.*

The DCA based on the abundance of shrubs and trees separated young landslides from intermediate and old landslides and the undisturbed forest along the first axis of the ordination but not along the second axis (Fig. 2). The abundance of *Styphelia tameiameiae* increased in young landslides, whereas the same was true for *Antidesma platyphyllum, Clermontia clermontioides, Hedyotis* cf. *terminalis, Myrsine lessertiana,* and *Perrottetia sandwicensis,* in the undisturbed forest sites (Fig. 2; Appendix). Species found in the intermediate and old landslides were shared either with young landslides (*Pipturus albidus, Dodonea viscosa, Pluchea symphytifolia,* and *Scaveola chamissoniana*) or the undisturbed forest (*Broussaisia arguta, Psychotria hawaiiensis, Clermontia hawaiiensis,* and *Coprosma ochraceae*). Three native species, *Cibotium glaucum, M. polymorpha,* and *S. pallida,* were found in all three landslide-age categories and the undisturbed forest.

Landslides were clearly separated from the undisturbed forest when plants were classified according to their status as native and alien species (Fig. 2). Most alien species were recorded in young and

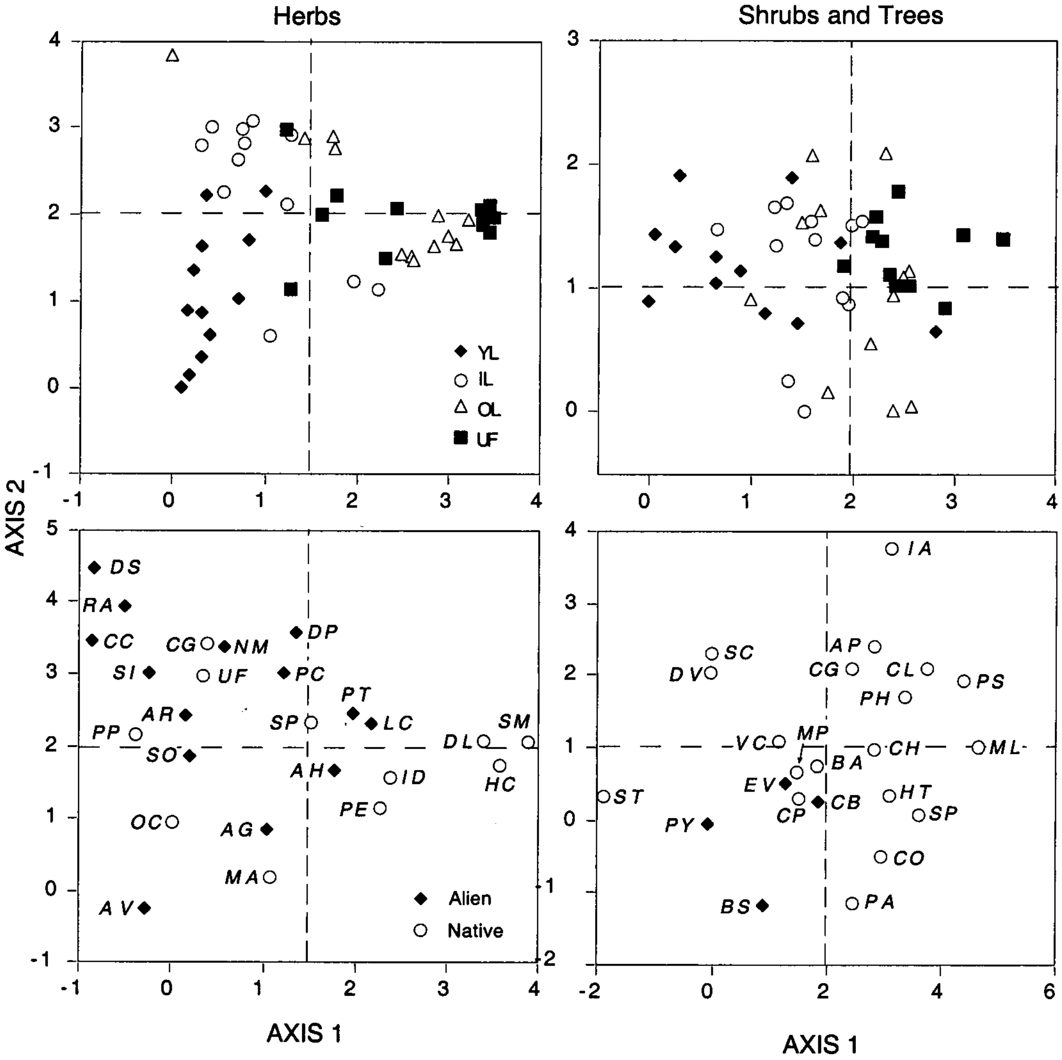

FIGURE 2. Ordination of samples and species along the first two axes generated by detrended correspondent analysis (DCA). DCA-axes are in standard units (SD); a distance of four units indicates that species composition varies significantly among samples. The upper panels show the ordination of the subplots, where YL = young landslides, IL = intermediate landslides, OL = old landslides, and UF = undisturbed forest. The lower panels show the ordination of the species. The dotted lines were drawn as reference points to compare pairs of figures (subplots and species) for each life-form. Abbreviations for the species are in the Appendix.

intermediate landslides, regardless of life-form (herbs, forbs, shrubs, or trees).

Alien species and plant establishment.—We recorded 31 species colonizing the clipped and bare rock quadrats (Appendix). Of these, 24 had established from seeds and spores and the remaining were resprouting (*e.g.*, grasses, sedges, and orchids). Six of the species that established from seeds were neither recorded before in our study plots nor along the trails that we frequented: they included 5 alien (*Ageratum conyzoides, Conyza canadensis, Crassocephalum crepidioides, Epilobium ciliatum,* and *Polygonum capitatum*) and one native (*Pseudognaphalium sandwicensium*) species. Three species (*Arundina graminifolia, P. capitatum,* and *Vaccinium calycinum*) recorded in August 1997 were absent from our plots by February 1998. Converse-

TABLE 2. *Seedling recruitment on three young (<18 yr) landslides in the Ninole ridges of Hawai'i one year after the experimental plots were established. Data for the three landslides were pooled for these analyses. Life-form includes trees (T), shrubs (S), and herbaceous plants (H). Alien species are identified with* [a]. *Significant at 5 (*), at 1 (**), and at 0.1 percent (***).*

Species	Life-form	Plots		G_{adj}
		Clipped	Bare rock	
No differences				
Dodonea viscosa	T	9	6	0.58
Machaerina angustifolia	H	8	12	0.79
Conyza bonariensis[a]	H	5	6	0.08
Group of aliens[1,a]	H	9	16	1.95
Bare rock > Clipped				
Pseudognaphalium sandwicensium	H	3	12	5.70*
Metrosideros polymorpha	T	75	133	15.94***
Sadleria pallida	T	2	46	49.38***
Pluchea symphytifolia[a]	S	88	119	4.50*
Rubus argutus[a]	S	13	30	6.83**
Lapsana communis[a]	H	1	24	25.75***
Epilobium ciliatum[a]	H	19	276	267.46***
Bare rock < Clipped				
Scaveola chamissoniana	S	15	1	14.28***
Ageratum conyzoides[a]	H	11	2	6.59*
Ageratina riparia[a]	H	206	94	47.49***
Cuphea carthagenensis[a]	H	73	25	24.32***

[1] To establish any effect of clipping or soil removal on plant recruitment, we analyzed each species by means of a goodness of fit (*G*) test. Sample sizes for six alien species did not satisfy the criterion that more than 80 percent of the expected cell frequencies have to be greater than 5; so we pooled them into a single group (Sokal & Rohlf 1995). These species were *Conyza canadensis, Crassocephalum crepidioides, Erechlites valerianifolia, Desmodium* sp., *Nephrolepis multiflora,* and *Anemone hupehensis.* We corrected the *G* values using the Williams correction, since goodness of fit tests involving two classes result in more type I errors than expected; the adjusted *G* values are more conservative than the non-adjusted ones (Sokal & Rohlf 1995).

ly, four species (*Conyza bonariensis, Desmodium* sp., *O. chinensis,* and *S. pallida*) were new to our plots in February 1998.

Clipping the vegetation or removing the vegetation and soil clearly had an effect on plant recruitment: 11 out of 15 species responded differently to the treatments. Given a 5 percent probability of having a species responding differently to the treatments, it is very unlikely that 11 or more species would have shown such a pattern by chance alone (binomial test: $P = 8.5 \times 10^{-11}$). Native species could be classified in three groups depending on their response to the treatments one year after establishment of the experiment (Table 2). One set of species, which included the sedge *M. angustifolia* and the treelet *D. viscosa,* was equally abundant in clipped and bare plots. A second group, which included *M. polymorpha,* was more abundant in bare rock than in clipped plots. Lastly, a third set that included the native *S. chamissoniana* was more abundant in clipped than in bare rock plots. Overall, seedlings of alien plant species outnumbered those of native species in terms of number of species (14 versus 6) and individuals (895 versus 322). Interestingly, the removal of alien grasses and orchids resulted in the recruitment of a group of alien species that had a reduced cover or were absent from our sites at the time the experiment was established (Table 2). *Epilobium ciliatum,* for example, was never recorded in our plots, but at the end of the experiment, 276 seedlings had recruited in the bare rock subplots (versus 19 in clipped subplots).

ESTABLISHMENT, SURVIVAL, AND GROWTH OF *M. POLYMORPHA* SEEDLINGS.—More seedlings of *M. polymorpha* recruited in bare rock than in clipped plots (goodness of fit test: $\chi^2 = 16.2$, $P < 0.01$; Fig. 3a; Table 2). Survival of transplanted *M. polymorpha* seedlings was higher in the control than in the clipped and bare rock quadrats (goodness of fit test: $\chi^2 = 5.9$, $P < 0.05$; Fig. 3b); growth of the transplanted seedlings of *M. polymorpha* was higher in the bare rock than in the clipped and control quadrats (ANOVA on logtransformed data: $F_{2,52} = 5.01$, $P = 0.01$; Fig. 3c).

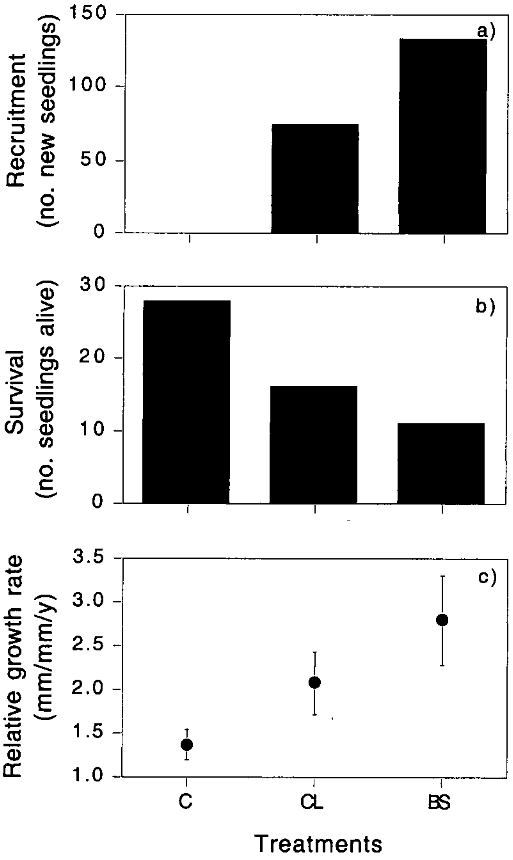

FIGURE 3. Treatment effects on (a) the number of naturally established *Metrosideros polymorpha* seedlings, (b) the number of transplanted *M. polymorpha* seedlings that remained alive, and (c) mean relative growth rates (mm/mm/yr) of transplanted *M. polymorpha* seedlings one year after the experiment was set up. C = control plots, CL = clipped plots, and BS = bare soil plots. Bars represent 1 SD.

DISCUSSION

Landslides and plant diversity on the islands of Hawai'i.—Our results clearly indicate that landslides are influencing plant diversity in the Ninole ridges of Hawai'i. Landslides may greatly alter successional trajectories, and thus species composition, by removing the tephra-derived soils and favoring the establishment of alien species. Landslides are increasing the diversity of the Ninole ecosystems in two ways. First, they are favoring the establishment of native species characteristic of early successional habitats. Second, they are favoring the establishment of alien species.

We were able to identify three distinct groups of plants. The first group found in areas disturbed by landslides included native and a high proportion of alien plant species; the second group found in the undisturbed Ninole forests included primarily native species. The third group found in landslides and the undisturbed forest included mostly native and some alien plant species. Native species colonizing young landslides, such as *D. viscosa, S. chamissoniana,* and *S. tameiameiae,* are found elsewhere in mesic to seasonal environments, growing on young lava flows or tephra-derived soils with various degrees of disturbance (Kitayama *et al.* 1995). Native species established in the undisturbed Ninole forests, such as *B. arguta, P. hawaiiensis,* and *Clermontia* sp., are found in mesic to wet environments, growing in the forest understory (Kitayama & Mueller-Dombois 1995, Kitayama *et al.* 1995). The occurrence of seedlings and saplings of these latter species only in the undisturbed Ninole forests suggests that they are forest specialists. Three species, *M. polymorpha* and the tree ferns *S. pallida* and *C. glaucum,* were represented among the three landslide-age categories and the undisturbed forest. These species not only colonize young lava and tephra substrates, they also persist and become the dominant species of Hawaiian mesic and wet montane ecosystems (Kitayama & Mueller-Dombois 1995, Kitayama *et al.* 1995).

The results of our experiments further supported this grouping of species. For example, *S. chamissoniana* was found along the edges of young landslides (10 edge *versus* 4 center individuals). In our experiment, seedlings of this species were more common on the clipped than on the bare quadrats (15 vs. 1), suggesting that *S. chamissoniana* favors the edges because of the presence of soil: seeds may be part of the seed bank and respond to increases in light levels once landslides occur and/or seeds are preferentially deposited in those sites by dispersers. Young *M. polymorpha* and *S. pallida* individuals were found both in the center and edges of young landslides. In our experiment, seedlings of these two species were more abundant in bare rock (N = 133) than in clipped (N = 75) quadrats, suggesting that they colonize and establish either on bare basalt or soil.

The only other studies in the Hawaiian islands that have investigated changes in species composition following the formation of landslides have been conducted in the much older (2500 kyr) Koolau Mountains, Oahu. Here, landslides in mesic sites are rapidly colonized by the false staghorn, *D. linearis* and some unidentified alien species; among the thick mats of *D. linearis,* scattered individuals of the trees *M. polymorpha, Cheirodendron trigynum, Pittosporum glabrum,* and *Acacia koa* and the tree fern *Cibotium* sp. emerge (Wentworth 1943, Scott 1969). In less mesic sites, landslides are colonized by the alien grass *A. virginicus* (Noguchi 1992). On the even older island of Kauai, landslides are covered rapidly by *D. linearis*; in recent years, the alien grass *S. condensatum* has colonized landslide-disturbed areas (E. Pettys, pers. comm.). Patterns of species composition on the Ninole landslides do not resemble those from the Koolaus and Kauai, probably because of differences in substrate that include the presence of little-weathered basalt and tephra-derived soils at Ninole.

Landslides may contribute to the establishment and spread of alien species into the Ninole ecosystems. First, a high proportion of the herbaceous species found on young landslides were aliens (Fig. 2). Second, the removal of the alien grasses and orchids resulted in the recruitment of a second group of aliens, mostly forbs. In our sampling plots, some of these forbs (*e.g., A. riparia* and *C. carthagenensis*) had a high cover. Lastly, recruitment and growth of *M. polymorpha* seedlings were higher in quadrats in which grasses and orchids were removed. These results suggest that the conditions in the undisturbed forest are not favorable for the establishment of alien species (*i.e.,* the undisturbed forest is "resistant" to the invasion of alien species). It is also possible that aliens may be replaced by native species over time, as indicated by their near absence from old landslides. Alternatively, our results may indicate that a combination of favorable conditions on young landslides and an increased presence of alien species in the area is driving the observed patterns. In fact, forest clearing around the Ninole ridges and the establishment of sugarcane plantations within the last 50 years may have favored the movement of aliens in this area. Our results indicate that the removal of tephra-derived soils by landslides in combination with an increased presence of alien species may greatly alter successional trajectories in the Ninole ridges of Hawai'i.

LANDSLIDES AND PATTERNS OF SPECIES DIVERSITY ELSEWHERE.—The few studies that have documented changes in species composition after disturbance by landsliding indicate that there is a narrow set of species that colonizes the young substrates; these species, however, vary from site to site (Guariguata 1990, Myster 1993, Dalling 1994, Myster & Walker 1997, Myster & Sarmiento 1998). In the Luquillo forest of Puerto Rico, the young landslides studied by Guariguata (1990) were colonized by shrubs and trees in the Rubiaceae and Cecropiaceae; alien species were never reported in spite of the fact that Puerto Rico has many alien plant species (M. Guariguata, pers. comm.). In the Las Mirlas watershed of Colombia, landslides are colonized by species in the Poaceae (including some alien species), Orchidiaceae, and Asteraceae as observed in the Ninole (C. Restrepo, pers. obs.). The Puerto Rican landslides are roughly at the same latitude and elevation as those in the Ninole, but the underlying geological substrate is different. On the other hand, the Las Mirlas landslides are at a similar elevation as those in the Ninole (after correcting for latitude) and share a similar geological substrate. At Las Mirlas, landslides have removed ash-derived soils and exposed basalts similar to those found in the Ninole. This leads to the suggestion that perhaps geological substrate may be important in explaining patterns of succession and diversity on landslides. More data, however, are needed to tease apart the role of climate, geological substrate, and floristic composition on succession after disturbance by landsliding.

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APPENDIX 1. *Plant species recorded in the Ninole ridges of Hawai'i. Young (Y), intermediate (I), and old (O) landslides, undisturbed forest (UF), and experimental plots on young landslides (EX). Species occurrences given in parentheses were observed in similar habitats but not recorded on the sampling plots. Alien species are identified with* [a].

	Species	Family	Y	I	O	UF	EX
AO	*Alyxia olivaeformis* Gaud.	Apocynaceae				(x)	
IA	*Ilex anomala* Hook. & Arnott	Aquifoliaceae				x	
TH	*Tetraplasandra hawaiiensis* Gray	Araliaceae				(x)	
AC	[a]*Ageratum conyzoides* L.	Asteraceae					x
AR	[a]*Ageratina riparia* (Regel) King & Robinson	Asteraceae	x	x	x		x
CA	[a]*Conyza canadensis* (L.) Cronq.	Asteraceae					x
CB	[a]*C. bonariensis* (L.) Cronq.	Asteraceae		x			x
CS	[a]*Crassocephalum crepidioides* (Benth.) Moore	Asteraceae					x
EV	[a]*Erechtites valerianifolia* (Wolf) DC	Asteraceae	x	x			x
LC	[a]*Lapsana communis* L. Gillis	Asteraceae		x	x		x
PY	[a]*Pluchea symphytifolia* (Mill.)	Asteraceae	x	x	x		x
PW	*Pseudognaphalium sandwicensium* (Gaudich.) Anderb.	Asteraceae					x
DP	[a]*Deparia petersenii* (Kunze) Kato	Athyriacae	x	x	x		(x)
SP	*Sadleria pallida* Hook. & Arn.	Blechnaceae	x	x	x	x	x
BS	[a]*Buddleia asiatica* Lour.	Buddleiaceae		x	(x)		
PS	*Perrottetia sandwicensis* Gray	Celastraceae				x	
CG	*Cibotium glaucum* (Sm.) Hook. & Arn.	Cyatheaceae	x	x	x	x	
	C. menziesii Hook	Cyatheaceae				(x)	
MA	*Machaerina angustifolia* (Goud.)	Cyperaceae	x	x	x	x	x
PP	*Pycreus polystachys* (Rottb.) Beauv.	Cyperaceae	x	x			(x)
ST	*Styphelia tameiameiae* (Cham. & Schlechtend.) F. v. Muell	Epacridaceae	x	x			
VC	*Vaccinium calycinum* Sm.	Ericaceae	x	x	x		x
	V. reticulatum	Ericaceae			(x)	(x)	
AP	*Antidesma platyphyllum* Mann	Euphorbiaceae				x	
CP	*Cyrtandra* cf. *Plati phylla* Gray	Gesneriaceae		x	(x)	(x)	
DL	*Dicranopteris linearis* (Burm.f.) Unerw.	Gleicheniaceae	x	x	x	x	
	Diplopterygium pinnatum	Gleicheniaceae		(x)			
SC	*Scaveola chamissoniana* Gaud.	Goodeniaceae	x	x	x		x
BA	*Broussaisia arguta* Gaud.	Hydrangeaceae		x	x	x	
DS	[a]*Desmodium* sp.	Leguminosae	x	x	x		x
OC	*Odontosoria chinensis* (L.) Sm.	Lindsaeaceae	x	x			x
CC	[a]*Cuphea carthagenensis* (Jacq.) Machr.	Lythraceae	x	x	(x)		x
CH	*Clermontia hawaiiensis* (Hillebr.) Rock	Lobeliaceae			x	x	
CL	*C. clermontioides* (Gaud) Heller	Lobeliaceae				x	
PE	*Palhinhaea cernua* (L.) Franco & Vasc.	Lycopodiaceae	x	x	x	x	
	[a]*Clidemia* ?	Melastomataceae		(x)			

APPENDIX 1. *Continued.*

	Species	Family	Y	I	O	UF	EX
ML	*Myrsine lessertiana* A.DC	Myrsinaceae				x	
MP	*Metrosideros polymorpha* Gaud	Myrtaceae	x	x	x	x	x
	[a]*Psidium cattleianum* Sabine	Myrtaceae		(x)			
NM	[a]*Nephrolepis multiflora* (Roxb.) Jarrett ex Morton	Nephrolepiadaceae	x	x	x	x	x
EC	[a]*Epilobium ciliatum* Raf.	Onagraceae					x
AG	[a]*Arundina graminifolia* (Don) Hochr.	Orchidiaceae	x	x			x
PT	[a]*Phaius tankarvilleae* Banks ex L'Hér.	Orchidiaceae		x	x	x	
	[a]*Spathoglothis plicata*	Orchidiaceae	(x)				
	Freycinetia arborea Gaud.	Pandanaceae				(x)	
	[a]*Passiflora ligularis* Juss	Passifloraceae		(x)			
AV	[a]*Andropogon virginicus* (L.)	Poaceae	x	x			(x)
ID	*Isachne distichophylla* Munro ex Hillebr.	Poaceae	x	x	x	x	
PC	[a]*Paspalum conjugatum* Bergius	Poaceae	x	x	x	x	(x)
SI	[a]*Sacciolepis indica* (L.) Chase	Poaceae	x	x			(x)
SO	[a]*Schizachyrium condensatum* (Kunth)	Poaceae	x	x	x		(x)
	[a]*Melinis minutiflora* Beauv.	Poaceae	(x)				
	[a]*Polygonum capitatum* Ham.	Polygalaceae					x
AH	[a]*Anemone hupehensis* Lemoine	Ranunculaceae	x	x	x	x	x
RA	[a]*Rubus argutus* Link	Rosaceae	x	x	x		x
CO	*Coprosma* cf. *ochraceae* Oliver	Rubiaceae			x	x	
HC	*Hedyotis centranthoides* (Hook. & Arnott) Steud.	Rubiaceae	x	x	x	x	
HT	*Hedyotis* cf. *terminalis* (Hook. & Arnott) Wagner & Herbst	Rubiaceae				x	
PH	*Psychotria hawaiiensis* (Gray) Fosb.	Rubiaceae			x	x	
	Melicope clusiifolia A. Gray	Rutaceae				(x)	
DV	*Dodonaea viscosa* Jacq.	Sapindaceae	x	x	x	x	x
SM	*Smilax melastomifolia* Sm.	Smilacaceae			x	(x)	
PA	*Pipturus albidus* (Hook. & Arnott) Gray	Urticaceae	x	x	x		
	Unknown	Fern		x			