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Early successional woody plants facilitate and ferns inhibit forest development on Puerto Rican landslides

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Summary

1. The experimental removal of early successional species can explain how plant communities change over time.

2. During a 7.3-year period, early successional woody species, scrambling ferns and tree ferns were removed from a total of 10 landslides in the Luquillo Experimental Forest in north-eastern Puerto Rico.

3. Early successional woody plants in combination with tree ferns decreased species richness and cover of forbs and increased richness of late-successional woody plants compared to removals, facilitating long-term forest development.

4. Dense stands of scrambling ferns decreased both forb and woody plant richness compared to removals, inhibiting forest development.

5. Stands of monospecific tree ferns initially increased woody plant richness compared to removals, but overall decreased woody plant richness and cover, inhibiting forest development.

6. *Synthesis*. Early successional species both facilitate and inhibit succession on tropical landslides, but detailed predictions of successional trajectories remain elusive and are influenced by stochastic processes including arrival order, the life-form of colonizing species and their competitive interactions.

Key-words: assembly, competition, disturbance, facilitation, Gleicheniaceae, primary succession, removal experiment, scrambling fern, tree fern, understorey plants

Introduction

Understanding how plant communities assemble and change over successional time following a disturbance remains a challenge (Walker & del Moral 2003). The development of community structure and function can be a deterministic process of filtering out plants that do not fit the physical or biotic environment, in which case species in a community would be more similar in functional traits than expected by random (Díaz & Cabido 1997). Alternatively, species presence in a community can be caused by a combination of stochastic dispersal and establishment processes (Hubbell 2001) combined with subsequent species interactions such as competition or facilitation (Callaway & Walker 1997), in which case differences in the pool of functional traits among successful species would be emphasized (Valladares *et al*. 2008). Deterministic and stochastic processes can simultaneously influence plant succession at different levels of organization (Walker & del Moral 2003).

The sorting of species by functional traits has led to insights about successional dynamics (Fukami *et al*. 2005) whereby species that arrive first often differ in seed mass, dispersal mode, growth rates and competitive abilities from later-successional species (Eviner & Chapin 2003). While single species or the outcome of pairwise interactions sometimes direct successional dynamics (e.g. a dominant nitrogen fixer introduced into a primary succession; Vitousek & Walker 1989), most successional trajectories are determined by the outcome of multiple species interactions. Interpretation and modelling of these interactions can be simplified by clustering species by similarity in form (as size and shape are closely linked to competitive superiority and resource acquisition) or function (e.g. leaf characteristics such as nitrogen [N] and phosphorus [P] content

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or decomposition rate; Ordoñez *et al.* 2009). However, not all analyses of structural or functional groups inform us about succession (Walker, Bellingham & Peltzer 2006), perhaps due to independent variation of multiple traits within species (Eviner 2004) or the complex and often random assembly of a temporally dynamic environment (Honnay, Verhaeghe & Hermy 2001).

Within a successional context, data are needed from disturbances such as tropical landslides that result in spatially heterogeneous patches, as these situations offer local contrasts in resource availability and potential insights into distinct patterns of plant colonization (van Coller, Rogers & Heritage 2000). Substrate texture (Larsen, Torres-Sánchez & Concepción 1999), stability (Velázquez & Gómez-Sal 2007) and fertility (Shiels *et al.* 2008) can all influence which species, functional groups of plants and life-forms colonize a disturbance. Two types of communities are typically the first to establish on stable portions of tropical landslides: an unpredictable mix of early successional woody plants (shrubs and trees) combined with tree ferns (4–8 + m tall) or dense stands of 1- to 3-m-tall thickets of vine-like, scrambling ferns in the Gleicheniaceae (Slocum *et al.* 2004). The successional implications of stands of these species (mixed or monospecific) on later-successional tree species are poorly understood. Tree fern stands can reduce erosion and facilitate the establishment of shade-tolerant tree species by providing establishment sites on their trunks (Gaxiola, Burrows & Coomes 2008). Tree ferns can also inhibit establishment or growth of trees through competition for nutrients (Vitousek *et al.* 1995) or light (Coomes *et al.* 2005). Scrambling fern thickets can slow soil erosion (Walker & Shiels 2008) and facilitate seed germination (Walker 1994), but also reduce species diversity (Kessler 1999), alter light and soil nutrients (Russell, Raich & Vitousek 1998) and inhibit the growth and establishment of trees (Slocum *et al.* 2004). Tropical landslides provide an ideal surface for examining the role of early successional woody plants and ferns because of their heterogeneous surfaces, variable suite of colonists and conditions conducive to rapid plant growth (Walker *et al.* 1996; Shiels, Walker & Thompson 2006).

In this study, we conducted three 7.3-year-long removal experiments on landslides in Puerto Rico to examine the effects of early successional species on the rates and trajectories of landslide succession. Specifically, we asked: (i) Do early successional woody plants and ferns alter species richness, vegetation cover and biomass in predictable ways? (ii) Do they affect nutrient or light availability? (iii) Do they inhibit the establishment of other functional groups of colonizing plants, including understorey plants? (iv) What are the successional implications of removing early successional plants, particularly regarding colonization by late-successional woody species?

Materials and methods

STUDY SITE

The Luquillo Experimental Forest in north-eastern Puerto Rico covers 11 000 ha (18°15–23′ N and 65°48–52′ W; 150–1000 m a.s.l.), has moderately high rainfall (3000–4000 mm year^{-1}) that varies more between than within years, and has mean monthly temperatures from 21 °C to 25 °C (Brown *et al.* 1983). The natural vegetation in our study area is considered subtropical lower montane wet forest *sensu* Holdrige (Ewel & Whitmore 1973) and is dominated by the tree *Dacryodes excelsa* (tabonuco). Nomenclature follows Liogier & Martorell (1982) and Little, Woodbury & Wadsworth (1974) for trees, Taylor (1994) for other flowering plants and Proctor (1989) and Smith *et al.* (2008) for ferns.

WOODY PLANT REMOVAL EXPERIMENT

We examined the successional implications of removing all early successional trees ($N = 5$ species), shrubs ($N = 14$) and dominant ferns ($N = 3$) on the four landslides that met our criteria of > 400 m^2 of mineral soil exposed in the last 3 months, road access and < 60° slope (Table 1; see also Appendix S1 and Tables S1 and S2 in Supporting Information for more information about this experiment). The ferns that we removed from 5 × 5 m plots were the tree fern

Table 1. Methods summary for the three removal experiments: woody plants, scrambling ferns (*Sticherus bifidus* and *Gleichenella pectinata*), the tree fern *Cyathea arborea*. NA, not applicable because no harvesting was made in the tree fern removal experiment. See Table S2 for details of woody plants removed

Methods	Woody plant experiment	Scrambling fern experiment	Tree fern experiment
Major species removed	All early successional woody plants and *Cyathea*	*Sticherus* & *Gleichenella*	*Cyathea*
Minor species removed (< 1% of biomass)	*Sticherus* & *Gleichenella*	*Cyathea*	*Sticherus* & *Gleichenella*
No. landslides	4	4	2
Age of landslides	1	15	19
No. plots per landslide	4	4	4
Plot size	5 × 5 m	3 × 3 m	8 × 8 m
No. pooled soil cores per plot	4	2	8
Light measurements	Hemiphotos	PAR	Hemiphotos
No. canopy profiles per plot	12	8	36
Leaf nutrients, litter biomass, litter nutrients	Yes	Yes	NA
Final harvest	Above ground	Above ground	NA

Cyathea arborea (L.) Sm. (hereafter *Cyathea*) and two scrambling ferns in the Gleicheniaceae, *Sticherus bifidus* (Willd.) Ching (formerly *Gleichenia bifida*; hereafter *Sticherus*) and *Gleichenella pectinata* (Willd.) Ching (formerly *Dicranopteris pectinata*; hereafter *Gleichenella*). Although *Cyathea* dominated in terms of removal biomass and frequency, both the scrambling ferns and *Cyathea* were a minor part of the final biomass in the controls (< 1% and 7.7 ± 2.5%, respectively); therefore, this experiment was essentially the removal of early successional woody plants. Because of the scouring effects of a landslide, this experiment resembled an exclusion experiment and therefore avoided most legacy effects typical of removal experiments (Peltzer *et al.* 2009). Removals were done semiannually from January 1998 to May 2005 followed by measurements of species richness and cover (as discrete classes) for forbs and woody plants, and cover of less-dominant ferns, graminoids and lycophytes (mostly *Lycopodiella*). Each January we sampled soils and analysed total Kjeldahl nitrogen (TKN), organic matter (SOM) and pH. In May 1998 and May 2005, we measured incident light with hemispherical photographs. In May 2005, we analysed N and P content of both live leaves and leaf litter of both seed plants and ferns of common species and recorded total litter depth before harvesting all above-ground plants in the plots.

SCRAMBLING FERN REMOVAL EXPERIMENT

We removed thickets of the scrambling ferns, *Sticherus* and *Gleichenella*, on four landslides chosen randomly from the 10 landslides that met our criteria of > 200 m^2 of a dense cover (30–200 cm deep) of *Sticherus* and/or *Gleichenella*, and with a slope of < 60° (Table 1; see also Appendix S1 and Table S1). Initial removal of all vegetation from 3 × 3 m plots (> 99% of initial biomass was scrambling ferns) was in January 1998, followed by removal of all scrambling ferns and *Cyathea* tree ferns (< 1% of biomass) twice yearly until May 2005. At each visit, we measured vegetation cover as in the woody plant removal, and each January we sampled soils. Instead of hemispherical photos we measured photosynthetically active radiation (PAR) each year. In May 2005, we analysed N and P content of leaves and recorded litter depth before harvesting all above-ground plants in the plots and in the woody plant removal experiment.

TREE FERN REMOVAL EXPERIMENT

We removed C*yathea* tree ferns from the two landslides with stands of *Cyathea* that were suitably large (> 1 ha), dense (> 80% cover) and tall (3–8 m) but not too steep (< 60° slope; Table 1; see also Appendix S1 and Table S1). Removal in January 1998 of all *Cyathea* (> 99% of initial biomass) and scrambling ferns (< 1%) from 8 × 8 m plots was continued twice yearly until May 2005. At each visit, we measured vegetation cover as in the previous experiments and sampled soils every January. We used hemispherical photos to measure incident light in 1998 and 2005. No leaf nutrients or litter depths were measured and no final harvests were conducted in this experiment due to logistical difficulties.

STATISTICAL ANALYSES

We used analysis of covariance (ANCOVA; Huitema 1980) to look for landslide and treatment (removal versus control) effects on changes of species richness and cover through time. In the woody plant experiment, we also examined the effect of volcaniclastic and dioritic soil types (Appendix S1, Table S1). The plot effect was also fitted to refer the error term of treatment, landslide and Treatment × Landslide to the true source of replication of these factors. Our dependent variables for the three experiments included species richness (forbs and woody plants); cover of forbs, woody plants, less-dominant ferns, graminoids and lycophytes; and soil chemistry (TKN, SOM and pH). To perform the analyses, we first examined the shape of the response functions between each of the dependent variables and time (as the covariate). Then, for those variables with linear or curvilinear response functions, we used linear or nonlinear (polynomial) generalizations of the analysis of variance, respectively (Kutner *et al.* 2004). Both linear and polynomial models were fitted. In the case of continuous dependent variables (i.e. species richness of forbs and woody plants, TKN, SOM and pH), we selected a normal distribution function and an identity link function (Agresti 2002). In the case of discrete multinomial dependent variables (i.e. cover of forbs, woody plants, less-dominant ferns, graminoids and lycophytes), we selected an ordinal-multinomial distribution function and a logit link function.

To evaluate if removals promoted colonization of the different functional groups of plants at the end of the study period (May 2005), two-way analyses of variance (ANOVAS) were performed where treatment and landslide were considered as independent variables. Dependent variables included biomass of forbs, early and late-successional woody plants, tree ferns, scrambling ferns, less-dominant ferns, graminoids, vines, bryophytes, lycophytes, and coarse and fine litter harvested on each plot in 2005. One-way ANOVAS were used to look for landslide differences among plant functional groups found only in control plots (early successional woody plants, scrambling and tree ferns). We used two-way repeated-measures ANOVAS (SigmaStat 2005; time, treatment, landslide) to examine incident light values. Tukey pairwise comparisons were used to examine treatment effects on late-successional woody plants, litter depth, biomass, N and P content for the woody plant and scrambling fern experiments. The data were log-, square root-, arcsine- or Box–Cox transformed when necessary to meet the assumptions of the respective analyses. Mean values are presented with standard errors. Where not otherwise stated, these analyses were performed using STATISTICA (Statsoft 2001) and the R environment for statistical computing (R Development Core Team 2004).

Results

WOODY PLANTS

All measured variables except graminoid cover changed (in a linear or quadratic pattern) over time during our 7.3-year woody plant experiment (Table S3). Species richness of forbs increased more rapidly in removal than control plots (Fig. 1a) and was greater on dioritic soils than on volcaniclastic soils (see Appendix S1, Table S1). Species richness of woody plants was greater in the control (containing both early and late-successional species) than in the removal plots (containing just late-successional species), but changed over time in a similar pattern in both treatments (Fig. 1d). Similarly, species richness of only late-successional woody plants over time was greater in the control (total of nine species; mean number of species = 5.1 ± 0.6) than in the removal plots (seven species; 1.9 ± 0.4; $P < 0.001$).

Forb cover increased earlier and more rapidly in removal than in control plots, but both values converged at the end of the experiment (Fig. 1g). Woody plant cover was higher in control (early and late-successional species) than in removal

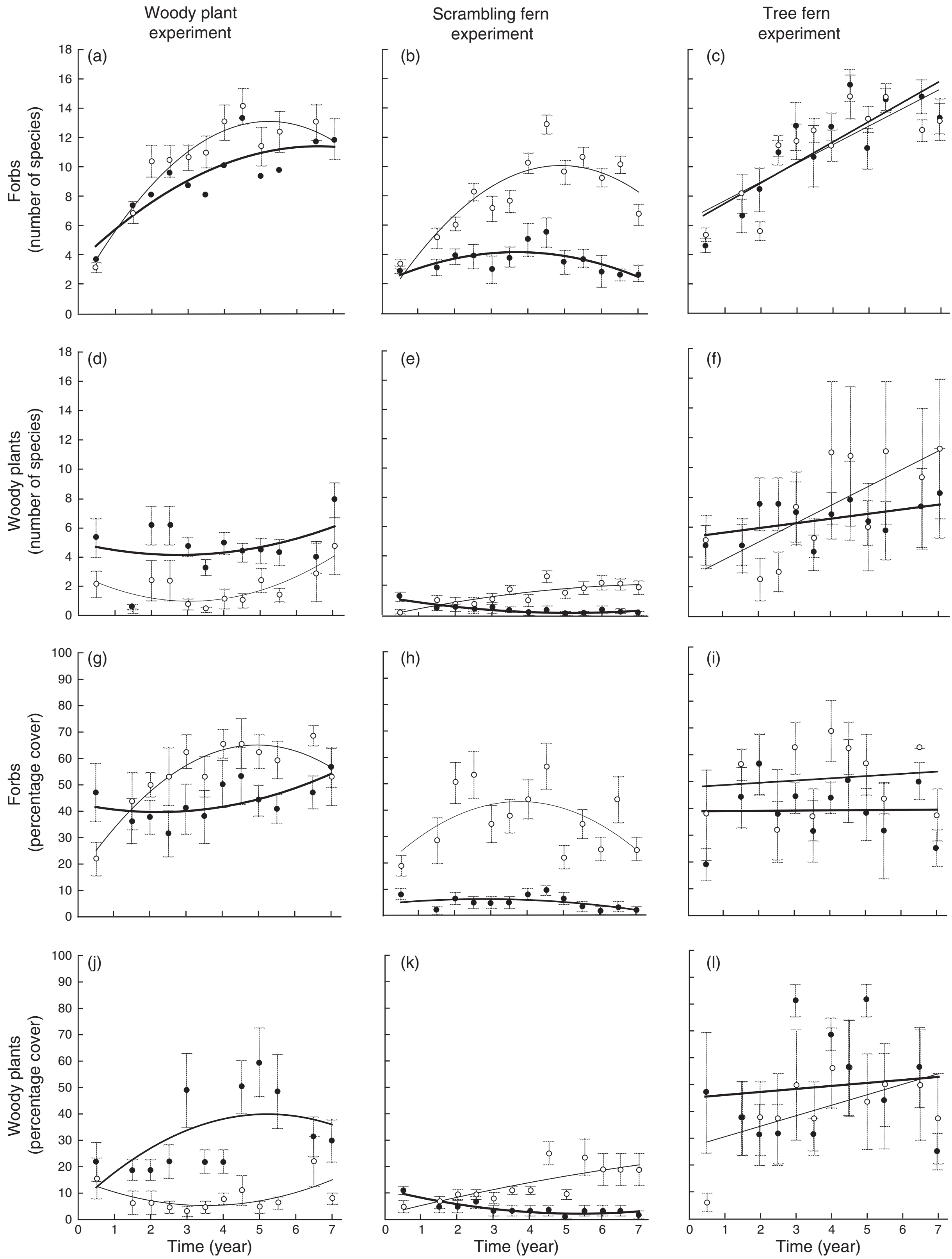

Fig. 1. Species richness or percentage cover measurements (mean ± SE) for (a) forb richness, (b) woody plant richness, (c) forb cover and (d) woody plant cover during the 7.3 years of the woody, scrambling fern and tree fern removal experiments for the removal (open circles) and control (filled circles) treatments. Lines (light for removal, bold for control) represent parameter estimates for linear or quadratic models.

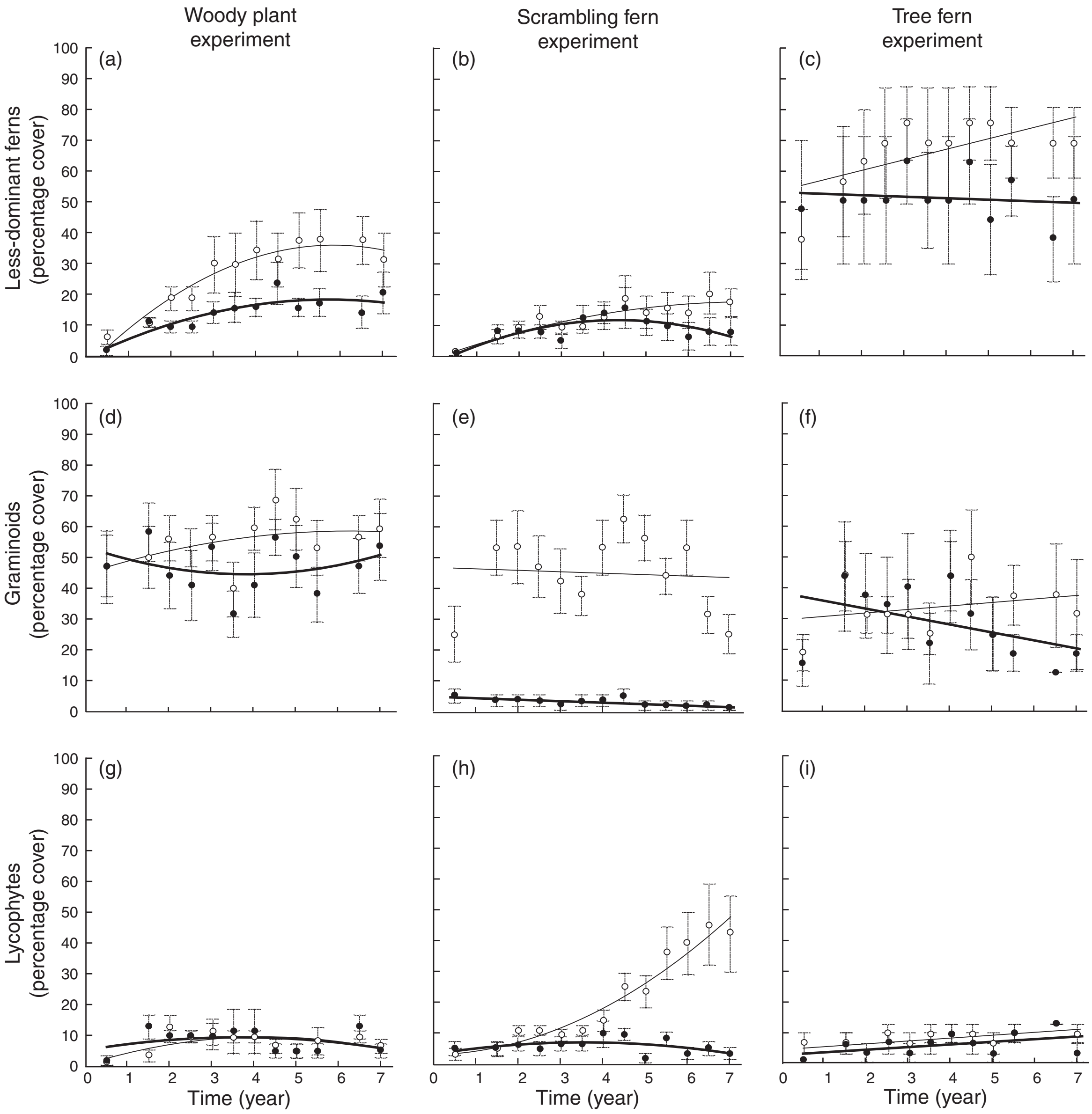

Fig. 2. Percentage cover measurements (mean ± SE) for (a) less-dominant ferns, (b) graminoids and (c) lycophytes during the 7.3 years of the woody, scrambling fern and tree fern removal experiments for the removal (open circles) and control (filled circles) treatments. Lines are described in Fig. 1.

plots (only late-successional species) and had different patterns of temporal change (Fig. 1j). Cover of less-dominant fern species (Fig. 2a) and graminoids (Fig. 2d) did not show treatment effects, although graminoids differed by landslides (Table S3). Cover of lycophytes had significant Time × Treatment and Landslide × Treatment interactions as it increased quickly in both removal and control plots, but then declined more rapidly in the removal than the control plots (Fig. 2g; patterns obscured by *y*-axis scale).

There were no treatment differences in soil variables (TKN, SOM and pH), but TKN ($F = 8.55$, $P = 0.007$) and SOM ($F = 15.32$, $P = 0.001$) differed among landslides (e.g. SOM was higher in volcaniclastic than dioritic soils). Values of transmitted light (global site factor; GSF) showed Landslide × Treatment interactions ($F = 4.75$, $P = 0.035$), decreased significantly over time ($F = 34.69$, $P < 0.001$) and declined differently among landslides (Landslide × Time interactions; $F = 4.40$, $P = 0.042$). Time × Treatment interactions were not significant ($F = 0.866$, $P = 0.366$), although absolute GSF values declined less in the removal (27%) than in the control treatment (41%).

Final biomass (Tables 2 and S4) varied little among landslides or between treatments, likely due to the high variance within and among landslides. For example, a single tree accounted for the biomass of late-successional plants in removal plots on one landslide and tree fern biomass was very unevenly distributed among control plots. However, fine litter mass was greater in the control than the removal treatment (Table 2), biomass of lycophytes and fine litter differed by landslides, and there were Landslide × Treatment interactions.

Table 2. Mean biomass (g m^{-2}), litter depth and litter N and P content in the woody plant and scrambling fern experiments from the final harvest at 7.3 years (mean ± SE; N = four landslides). Significant treatment differences (P < 0.05) are in bold. R, removal; C, control; NA, not applicable. Additional data are in Tables S4 and S5

	Woody plant experiment		Scrambling fern experiment	
Treatment	R	C	R	C
Functional group biomass (g m^{-2})				
Forbs	145 ± 77	82 ± 32	**31 ± 14**	**0.4 ± 0.4**
Early successional woody	0	2351 ± 1264	**49 ± 5**	**3 ± 3**
Late-successional woody	1734 ± 1091	4348 ± 1689	6 ± 6	0 ± 0
Tree ferns	0	831 ± 485	0	5 ± 5
Scrambling ferns	0	24 ± 23	0	1056 ± 194
Less-dominant ferns	1163 ± 1096	11 ± 4	33 ± 16	3 ± 3
Graminoids	102 ± 26	50 ± 28	72 ± 24	0 ± 0
Vines	6 ± 2	5 ± 2	1 ± 1	3 ± 2
Lycophytes	5 ± 3.2	9 ± 5	**149 ± 78**	**3 ± 2**
Fine litter	**3 ± 1**	**5 ± 2**	**2 ± 1**	**11 ± 3**
Total biomass	3159 ± 1684	7717 ± 3297	**345 ± 51**	**1079 ± 390**
Litter characteristics				
Depth (cm)	1.3 ± 0.6	1.9 ± 0.6	1.8 ± 0.8	8.0 ± 2.5
N (mg g^{-1})				
Fern leaves	10.1 ± 1.2	8.2 ± 0.7	6.4 ± 0.6	5.0 ± 0.3
Seed plant leaves	12.7 ± 3.0	11.2 ± 0.7	**7.4 ± 0.5**	**9.1 ± 0.6**
P (mg g^{-1})				
Fern leaves	0.5 ± 0.1	0.5 ± 0.0	0.3 ± 0.0	0.2 ± 0.1
Seed plant leaves	0.5 ± 0.1	0.6 ± 0.1	0.2 ± 0.1	0.2 ± 0.1

Among variables only found on control plots, early successional woody plants and tree ferns both varied by landslide. There were no treatment differences during the May 2005 harvest for litter depth, N and P concentrations (Table 2), although 24 of 32 possible treatment comparisons of leaf tissues (from the same species on the same landslide) had higher N or P values in control than in removal plots.

SCRAMBLING FERNS

Most variables in the scrambling fern experiment had significant Time × Treatment interactions. Forb, woody and total species richness values were significantly higher in removal than in control plots (Table S3; Fig. 1b,e) with temporal increases in removal plots and either decreases (woody richness) or little change (forb richness) in the control plots.

Cover of forbs and woody plants reflected patterns of richness, with higher values in removal than in control plots, increasing cover in removals and decreasing or constant cover values in controls (Table S3; Fig. 1h,k). Cover of less-dominant ferns had a significant Time × Treatment interaction with a consistent increase over time in the removal plots and an increase followed by a decrease in the control plots (Fig. 2b). Graminoid and lycophyte cover had a significant Time × Treatment interaction, increasing dramatically in removal plots, but not in the controls (Fig. 2e,h).

Soil TKN, SOM and pH did not differ by treatment in the scrambling fern experiment, although pH differed among landslides (F = 12.39, P < 0.001). Transmission of PAR to the ground surface remained consistently higher in the removal than in the control plots (F = 11.85, P < 0.001) and decreased significantly over time (F = 8.99, P = 0.002).

Final biomass of forbs, early successional woody plants, graminoids and lycophytes was higher in removal than control plots (Tables 2 and S5) and graminoids and lycophytes also had significant differences by landslide and by treatment within landslide. Fine litter mass was consistently higher in the control than the removal plots (Table 2). Scrambling fern biomass (part of the removal treatment) was consistently high (mean = 1056 ± 194 g m^{-2}) in the control plots and differed by landslide, but tree ferns were only present in one landslide (5 g m^{-2}). These treatment differences during the May 2005 harvest were due to higher biomass of ferns in the controls than in the removals. Leaf N and P were higher in controls than removals in 8 of 12 possible comparisons (of the same species on the same landslide). The N content of fern leaves in the litter was slightly higher in removal than control plots (P = 0.08), but in contrast, the N content of leaf litter of seed plants was higher in controls than removals (P = 0.02; Table 2).

TREE FERNS

Only a few measured variables in the tree fern experiment changed significantly through time and differed among treatments or landslides (Table S3). Forb and woody plant species richness increased during the study period, and woody species richness increased more rapidly in removal than control plots, although in the first few years, woody plant richness was higher in controls (Fig. 1c,f). Woody species richness also differed among landslides. There were no landslide, treatment or time differences for the cover of forbs (Fig. 1i), woody plants

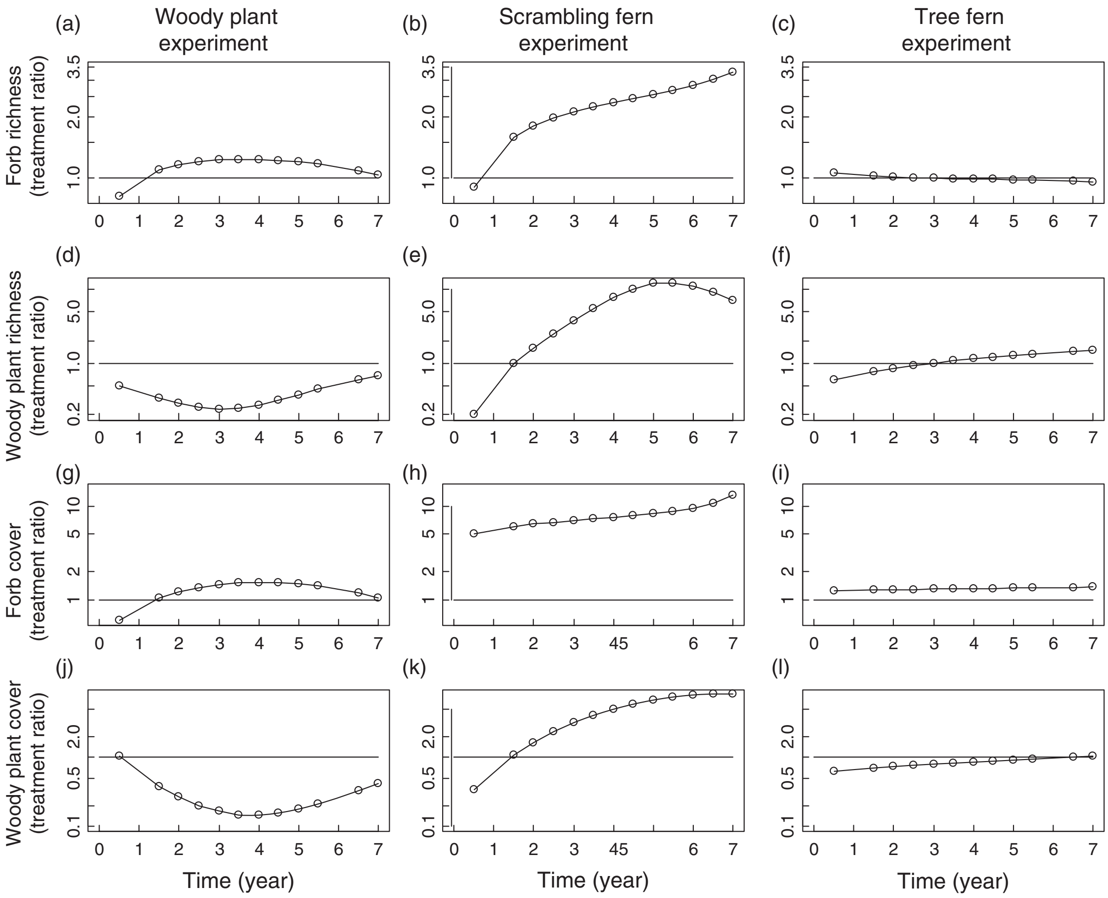

Fig. 3. Temporal trends in the relative effects of the treatment in each of the woody, scrambling fern and tree fern removal experiments, expressed as the ratios of the ANCOVA fitted values of the removal treatment to the control, for (a–c) forb species richness, (d–f) woody species richness, (g–i) forb cover and (j–l) woody plant cover during the 7.3 years of observation. The horizontal line represents a 1 : 1 ratio. The *y*-axis is logarithmic.

(Fig. 1l), less-dominant ferns (Fig. 2c), graminoids (Fig. 2f) or lycophytes (Fig. 2i).

Soil TKN decreased with time (quadratic pattern; $F = 12.75$, $P < 0.001$) and soil pH was lower in control than in removal plots due to significant Landslide × Treatment ($F = 12.18$, $P = 0.025$) and Time × Treatment ($F = 14.21$, $P < 0.001$) interactions. GSF values (light transmission) declined slightly in both treatments and did not differ among landslides or between treatments.

COMPARISONS ACROSS EXPERIMENTS

We compared experiments with ratios of removal to control results for richness and cover variables (Figs 3 and 4). The woody plant experiment showed divergent patterns during the first half of the experiment, with maximal treatment differences in the middle, and increasing resemblance (ratios approaching 1) between the treatments at the end of the experiment. In contrast, the scrambling fern experiment showed distinct divergence for most measured variables, with higher richness and cover in the removal plots that generally continued to increase throughout the experiment. The ratios for the tree fern experiment were never large, and both convergent and divergent patterns were observed.

Discussion

Early successional species have key roles to play in determining community assembly and successional trajectories, but this role is strongly influenced by their positive and negative interactions with other plant species (Callaway & Walker 1997). In our three experiments on landslides in a Puerto Rican rain forest, influential colonists were those with the highest relative biomass: early successional woody plants, a tree fern (*Cyathea arborea*) and scrambling ferns (*Sticherus* and *Gleichenella*). When dense stands of these three functional groups were removed, they were replaced by a more diverse and often dense mixture of forbs, less-dominant species of ferns, graminoids and lycophytes, highlighting the inhibitory role of thicket-forming species during early primary succession (Walker *et al.* 1996). Facilitative effects were also found, such as the higher incidence of late-successional woody seedlings in the woody plant controls. Thicket effects on light were more readily apparent than their impacts on soil resources or plant nutrient status, and the long-term impacts of thickets on forest succession are perhaps indirectly facilitative by reducing growth of herbaceous plants that inhibit forest seedling establishment.

The natural heterogeneity of landslide conditions both within and among experiments and variations imposed by our

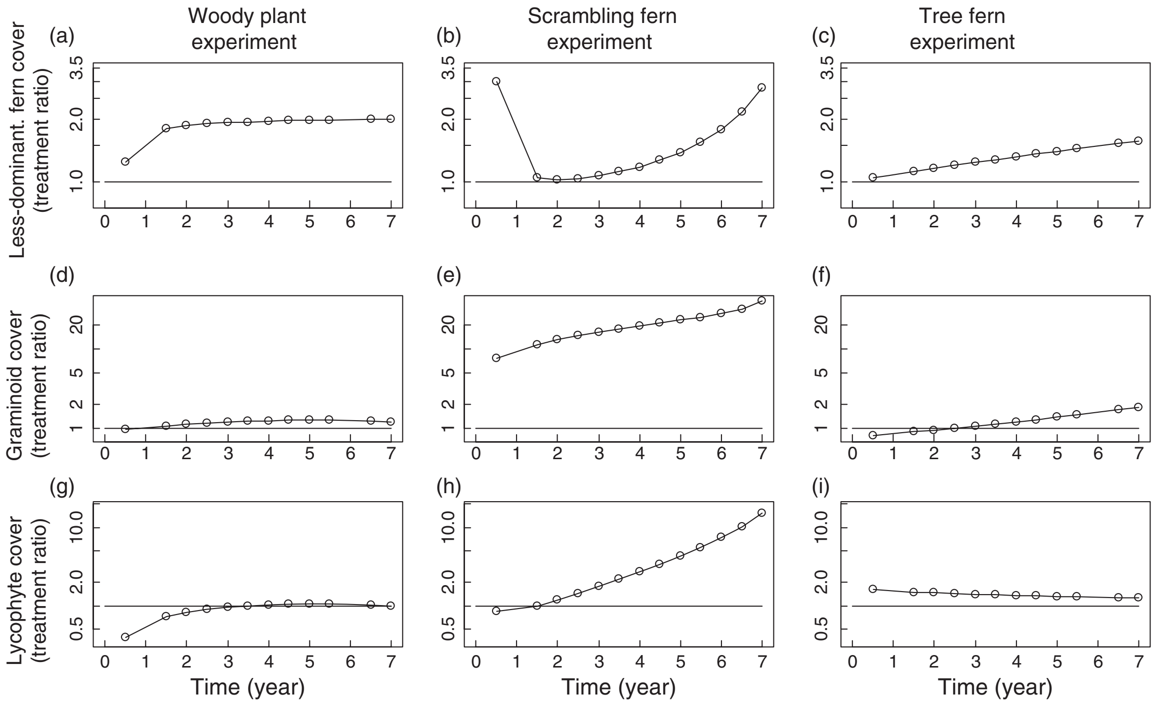

Fig. 4. Temporal trends in the relative effects of the treatment in each of the woody, scrambling fern and tree fern removal experiments, expressed as the ratios of the ANCOVA fitted values of the removal treatment to the control, for (a–c) less-dominant ferns, (d–f) graminoid cover and (g–i) lycophyte cover during the 7.3 years of observation. Lines and axes are described in Fig. 3.

treatments suggest caution in making broad interpretations of the successional role of different functional groups. Forest-level outcomes averaged over larger temporal and spatial scales than our 7.3-year study can be influenced in unexpected ways by single patches of particular species. Physical removals of scrambling and tree ferns involve potential disruption of soils and drainage as well as the removal of targeted species, whereas the woody plant experiment was effectively an exclusion experiment with minimal disruption. Low replication (n = 2 landslides) in the tree fern experiment may not have adequately represented the variation in these older landslides. Nevertheless, significant treatment, landslide and time differences were found in each experiment and contrasts among experiments can serve as useful guides for the interpretation of the role of the functional groups of plants represented across all experiments.

RICHNESS, COVER AND BIOMASS

The main direct impact of excluding 19 species of early successional woody plants and one species of *Cyathea* in the woody plant experiment was to allow the growth of vigorous thickets of forbs, less-dominant ferns and graminoids. However, generalizations are difficult due to stochastic factors that lead to 10- to 100-fold differences among landslides in how final biomass was distributed among the functional groups that invaded the removal plots. One landslide had several large individuals of another tree fern (*Cyathea portoricense*). Several (early and late-successional) woody plants contributed disproportionately to different landslides, and the total biomass among landslides in both treatments varied from 312 to 14 535 g m^{-2} (Table S4). Biomass of removal plots therefore ranged from 9% to 62% of the biomass of control plots, largely depending on the presence or absence of a few large plants. Nonetheless, richness and cover (and in most cases, biomass) of herbaceous species increased rapidly in our removal plots and generally exceeded values in control plots. In the control treatments, various fast-growing woody species (and accompanying *Cyathea*), reduced herbaceous ground cover and increased richness of late-successional woody plants relative to the removal treatments, suggesting a net facilitative effect of early successional woody plants on the establishment and growth of late-successional woody plants.

Removal of dense thickets of scrambling ferns led to dramatically increased richness of forbs and woody plants and increased cover and biomass of forbs, early successional woody plants, less-dominant ferns and lycophytes. Late-successional woody plants were occasionally present in removals but absent from control plots. In two of our four scrambling fern landslides, lycophytes dominated in both cover and biomass by the end of the experiment, reaching 63% and 77% of total biomass, respectively. Lycophytes, typically associated with disturbance (Tessier 2007), are adapted to the same xeric, infertile conditions in which the scrambling ferns thrive, perhaps due to guild proportionality (Holdaway & Sparrow 2006). The few lycophytes that survived in the control plots under the scrambling fern thicket were able to spread via rhizomes into the removal plots. It is unclear how long the lycophytes will dominate, but they are much less dense than the scrambling ferns that clearly inhibit establishment of later-successional woody species.

The removal of a 4- to 8-m-tall canopy of *Cyathea* ferns from 19-year-old stands had an initially negative, but net positive, effect on woody plant richness, and this was reflected in a rapid increase in plant cover in the removal plots as existing woody seedlings grew taller. The early successional woody species (10 in removal, 9 in control) were mostly the same species in both treatments, but late-successional woody species (10 in removal, 7 in control) mostly differed between treatments (L. Walker, unpublished data). The removal treatment favoured a different and larger suite of late-successional woody plants than the control, suggesting that tree ferns have a net negative effect on woody plant establishment.

NUTRIENT AND LIGHT AVAILABILITY

We conducted our woody plant experiment on two geological substrates that impacted several variables, including SOM, soil pH, forb and woody plant richness and cover of lycophytes. These results indicate the importance of substrate in successional dynamics (cf. Shiels *et al.* 2008), but do not clarify the role of the manipulated species in contributing to these variables, as few of the landslide type variables that were significant coincided with variables that had significant treatment effects.

Although soil variables did not vary by treatment, leaf N and P concentrations in the woody plant and scrambling fern experiments, as well as leaf litter N in the scrambling fern experiment, were generally higher in control than removal plots, suggesting a positive link between the much higher fern and fern litter biomass in control plots and the nutrient status of other plants. Tree ferns and scrambling ferns are capable of large accumulations of nutrients, often disproportional to their biomass (Vitousek *et al.* 1995; Russell, Raich & Vitousek 1998) and their lignin-rich litter is often slow to decompose (Shiels 2006; Richardson & Walker 2010), so they can serve as nutrient sinks for the ecosystem. By the end of our study, soils in the scrambling fern experiment had more SOM ($15.6 \pm 0.4\%$) than those in the initially bare woody plant experiment ($11.1 \pm 0.3\%$), but the soils in the tree fern experiment, vegetated for the longest period, had only accumulated $9.3 \pm 0.3\%$; soil N levels did not vary between treatments. Clearly, initial soil conditions and vegetative effects on soil fertility are confounded, and how soil fertility governs colonization is complex. Scrambling ferns can also reduce nutrient loss by preventing soil erosion (Walker & Shiels 2008). The paucity of treatment effects on soil parameters, despite the strong temporal changes in vegetation and the limited effects on plant tissues, suggests a great deal of functional redundancy in the vegetation that colonizes the removal or a long-term lag effect of our treatments (Slocum *et al.* 2006) that we did not account for in 7.3 years.

Forest succession rapidly reduces light levels and is certainly a factor in determining woody plant species replacements (Everham, Myster & VanDeGenachte 1996). Tree ferns (Coomes *et al.* 2005) and scrambling ferns (Russell, Raich & Vitousek 1998) can also impact succession through their diminution of light levels. While all of our experiments reflected a decrease in light over time, treatment effects were only found in the scrambling ferns where the removals had consistently higher light levels than the very densely vegetated controls (Walker 1994). Edge effects probably confounded our treatment results in the woody plant and tree fern experiments due to inadequate buffers proportional to the rapid growth of early successional plants and occasional proximity to mature forest. Nevertheless, decreasing light levels are a key factor in driving tropical plant succession on landslides (Fetcher *et al.* 1996).

SUCCESSIONAL IMPLICATIONS

Almost every variable we measured in the woody plant and scrambling fern experiments changed significantly over the 7.3-year study, suggesting a dynamic tropical ecosystem that results in a number of successional trajectories (Myster & Walker 1997). On Puerto Rican landslides, primary succession follows a broadly recognizable pattern where 19 early successional woody species and one tree fern colonize landslides in various combinations, while two species of scrambling ferns dominate other landslides. Then, within several years to many decades, later-successional forest trees colonize and eventually replace the early colonists (Walker, Velázquez & Shiels 2009). Locally, the spatial and temporal changes in species replacements are highly stochastic and the species composition or even life-form of later colonists is difficult to predict, particularly when chance establishment of single woody plants can alter local dynamics. Alternatives to forest succession include arrested stages dominated for decades by tree ferns, scrambling ferns, woody shrubs, vines or even sparse grass (Walker 1994; L. Walker, pers. obs.). Successional development on landslides is therefore broadly predictable with the replacement of an early successional functional group by a late-successional functional group (Fetcher *et al.* 1996), but within each group there is redundancy and thus potential stochasticity (Walker *et al.* 2003).

We found evidence for both facilitative and inhibitory interactions among functional groups. Early successional trees, well-known colonizers of disturbance (Denslow *et al.* 1990; Brokaw 1998), inhibited the establishment and growth of scrambling ferns and other herbaceous plants, thereby indirectly facilitating the establishment of late-successional tree species. This effect may accelerate the rate of succession, although our study was neither long enough nor extensive enough to confirm this possibility. Early successional trees can also inhibit tree ferns (Kessler 1999), but our study did not test for that possibility either. Three other functional groups slowed the rate of successional change through inhibition. Firstly, thickets of scrambling ferns dominated many landslide patches, perhaps through their tolerance of nutrient and/or drought stress (Hietz 2010). Shade from adjacent forest overstories may be what finally kills these remarkably persistent thickets. Secondly, thickets of tree ferns had a net negative effect on late-successional woody plants, except when in mixed stands with early successional woody plants that apparently offset their negative effect. Tree ferns can rapidly colonize disturbances due to prolific spore production (Conant 1976) and often out-compete woody plants on landslides (Kessler 1999; Slocum *et al*. 2006). The competitive advantage of tree ferns might be due to rapid uptake and slow recycling of nutrients as well as the inhibition of tree seedling establishment by the production of a thick litter layer on the forest floor (Drake & Pratt 2001). The final functional group that had inhibitory effects was the herbaceous understorey of forbs, less-dominant ferns, graminoids and lycophytes (cf. Velázquez & Gómez-Sal 2009) that were very responsive to our treatments and dominated the cover and even biomass on some landslides.

Conclusions

Our direct manipulations of vegetation on Puerto Rican landslides during a 7.3-year period have confirmed critical facilitative roles of early successional woody plant species and inhibitory roles of scrambling ferns and tree ferns in directing rain forest succession. While detailed prediction of successional trajectories is still elusive, the importance of arrival order, life-form and competitive interactions of early successional species is readily apparent (Glenn-Lewin, Peet & Veblen 1992). That ferns are key players in these systems is not surprising, given their rapid dispersal, tolerance of a variety of environmental conditions and competitive use of available resources (Mehltreter, Walker & Sharpe 2010). Long-term observations and manipulations of succession help identify critical steps in vegetation development that direct future change, supporting the observation that species composition is largely stochastic while eventual forest development is deterministic.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Supplementary methods and literature cited.

Table S1. Landslide characteristics.

Table S2. Woody species and ferns removed from woody plant experiment.

Table S3. ANCOVA results for all three experiments.

Table S4. Woody experiment landslide-specific final biomass.

Table S5. Scrambling fern experiment landslide-specific final biomass.

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