Seed Predation, Disease and Germination on Landslides in Neotropical Lower Montane Wet Forest

Randall W. Myster


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Seed predation, disease and germination on landslides in Neotropical lower montane wet forest

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Abstract. Seed mortality (caused by predators and pathogens) and germination were compared between Puerto Rico and Costa Rica on landslides in lower montane wet forest. Seeds of six common species on five Puerto Rican landslides and four common species on two Costa Rican landslides were used with a Cecropia species and a Gonzalaguina species included at both sites. In the Puerto Rican experiments Cecropia schreberiana was the only species to show significant seed predation (which was due to insects), pathogens grew from all species and fewer seeds were lost to predators than pathogens. Also in Puerto Rico mean germination across all species was 57% before dispersal (filled seeds collected while still on the tree) and 71% after, with Phytolacca rivinoides seeds germinating most abundantly, followed in descending order by Ocotea leucocysta, Cecropia spec., Miconia racemosa, Palicourea riparia and Gonzalaguina spicata. In the Costa Rican experiments three species had significant predation: Cecropia polyplebeia and Urera caracasana (both due to insects) and Witheringia coccoboides (due to mammals); pathogenic disease caused more seed loss than predation, and germination was high (61% pre-dispersal, 69% post-dispersal).

Similarities between these island and mainland sites included (1) percentage of seeds lost to predation and percentage lost to pathogens (all in the 5 - 15% range), (2) generalist pathogens which claimed more seeds than predators and (3) majority germination with a general increase after dispersal. Finally sites were dissimilar only in the number of species with significant predation loss and whether it was by insects or mammals, casting doubt on the traditional island/mainland dichotomy.

Keywords: Costa Rica; Disturbance; Island vs. Mainland; Montane forest; Puerto Rico; Regeneration; Seed dynamics.


Introduction

Biotic responses to disturbance, particularly to severe disturbance (Garwood et al. 1979; van der Maarel 1993), help determine ecosystem structure (Watt 1947; Brokaw 1985; Pickett & White 1985; Brokaw & Walker 1991). Landslides are among the most severe neotropical disturbances (Waide & Lugo 1992), removing organic matter and topsoil, exposing bare rock and shallow subsoils, and generating extreme environmental gradients (Fernández & Myster 1995; Myster & Fernández 1995). On a larger landscape scale, landslides may help maintain biodiversity, for instance by creating regeneration sites for rare species and ferns (Walker 1994) or acting to restock less severe but more frequently disturbed areas such as hurricanes (Willig & Camilo 1991) and influence nutrient cycling and material flow/redistribution (Swanson et al. 1982; Guariguata 1990).

Understanding island ecosystem structure has always included comparisons with the mainland and often stressed species richness differences due to (1) habitat diversity, (2) island size and distance to and diversity of the mainland, (3) immigration and extinction rates, or (4) island ‘samples’ of the mainland (Martin et al. 1995). In addition the strength of species interactions has been part of this comparison (Janzen 1973; Kitayama & Mueller-Dombois 1995). However island/mainland differences in disturbance regime has been missing in these studies and may be critical to understanding ecosystem structure on both (Sugden 1992). Because neotropic islands differ from the mainland in hurricane (Vandermeer et al. 1990; Brokaw & Walker 1991) and treefall gap frequency and dynamics (Brokaw 1985; Lawton & Putz 1988), landslides may be the natural disturbance which occurs in the most places. Consequently, I examine biotic responses after landslides because they may be useful in illuminating insular/continental similarities and differences, and, therefore, provide a good framework for comparison.

The little regeneration from saplings, seedlings or even from the seed pool in landslides (Guariguata 1990; Myster 1993b; Myster & Fernández 1995; Walker et al. 1997) points to a seed-driven revegetation process, where seed dispersal (Walker & Neris 1993), seed mortality mechanisms and seed germination are filters (Myster 1993a). Therefore, this study focuses on seed-oriented field experiments on landslides both in Puerto Rico and
Costa Rica and addresses these questions:
1. What are the effects of predation (invertebrate and vertebrate) and fungal disease on seeds collected directly from the tree (pre-dispersal) and on seeds placed on landslides (post-dispersal)? Also, is germination affected by dispersal?
2. How do seed predation, seed disease, and seed germination vary among tree species, compared to within and among landslides?
3. How do the levels of predation, disease and germination differ between Neotropic island and mainland landslides with similar life-zones (lower montane wet forest) and flora?

**Methods**

**Study sites and species**

The Neotropic island study site was the Luquillo Experimental Forest (LEF), a Long-Term Ecological Research site of the U.S. National Science Foundation, in the northeastern corner of Puerto Rico, USA (18° 20' N, 66° 00' W). Within the LEF, this study concentrated on the lower montane wet forest (Ewel & Whitmore 1973) characterized by Dacryodes excelsa (tabonuco), Cyrilla racemiflora (palo colorado) and Prestoea montana (sierra palm) (Waide & Lugo 1992). Common landslide vegetation includes the ferns Cyathea arborea and Gleichenia bifida in the bare soil areas and Cecropia schreberiana, Miconia racemosa, and Nepsera aquatica in the lower debris areas (Myster & Fernández 1995). Five landslides were selected: ES2 and ES3 in the Rio Espiritu Santo watershed (both < 5 yr old), RB2 and RB9 in the Rio Blancos watershed (15 and < 5 yr old, respectively), and one in the Bisley watershed (< 5 yr old). All are close to 2000 m² in size with the exception of RB2 which is 25,000 m² (Myster & Walker in press). In addition all landslides are between 500 and 600 m in elevation and, except for Rio Blancos landslides – which are on diorite intrusions – have soils derived from volcanoclastic primary substrate that has weathered into clay Ultisols (Walker 1994).

The seeds used in the LEF experiments came from the genus Cecropia, which may then moderate environmental extremes for the other woody test species which follow (Myster & Walker in press). All species are abundant in both vegetation (Myster & Walker in press) and seed rain on LEF landslides (Walker & Neris 1993).

The Neotropic mainland study site was the Monteverde Cloud Forest (MCF) Reserve of Costa Rica (10° 12' N, 84° 42' W). The MCF is dominated in the overstory by Lauraceae, Moraceae and Araliaceae, and in the understory by Rubiaceae, Solanaceae, Acanthaceae, Gesneriaceae, Piperaceae and Arecales (Palmae) (Lawton & Dryer 1980). Landslide vegetation is dominated by Gunnera insignis in the bare soil areas and Chusquea pohlii, Cecropia polyphlebia, and Palicourea standleyana in the lower debris areas (Myster 1993b). MCF has well-weathered soils of volcanic origin.

The climates of both LEF and MCF are dominated by trade winds that produce moisture-bearing clouds year-round (Odum & Pigeon 1970; Nadkarni & Matelson 1991). Total water input is similar between the two sites, although MCF receives more moisture deposition from mist-bearing winds (MCF averages 3.3 m/yr with 2.5 m/yr as rain and 0.8 m/yr as deposition; LEF averages 3-5 m/yr, almost all in rainfall with small amounts in deposition; Nadkarni & Matelson 1991; D. Schaefer pers. comm.). In addition, LEF has a dry season between late spring and summer and MCF has a dry season during the first few months of the year (Holdridge 1967; Lawton & Dryer 1980; Janzen 1983). Normal wind speeds above the canopy also have overlapping ranges (MCF 5 - 15 km/h; LEF 2 - 10 km/h; Brown et al. 1983; Nadkarni & Matelson 1991).

As a further indicator of the site similarity, the majority of tree genera found in Puerto Rican landslides also occur in Costa Rican landslides, and, therefore, the LEF landslide flora appears to be a large subset of the MCF landslide flora, at least at the generic level (Myster 1993b). Because of this floristic similarity and in order to magnify comparisons, test species were chosen to include a species of the genus Cecropia and a species of the genus Gonzalagunia at each site. The seed species used in the MCF experiments were Cecropiapolyphlebia, Gonzalagunia kallunkii, Urera caracasana and Witheringia coccoboides which are common species in Costa Rican landslide seed rain and vegetation (Myster 1993b) and may fill similar ecological roles as LEF landslide species of the same genera. Cecropia is both bird and mammal-dispersed; the other species are bird-dispersed.

The two landslides studied at MCF were in the Rio Penas Blancos watershed at 1300 m, approximately 2000 m² in size and were 5-15 yr old (M. Marin pers. comm.). Although MCF landslides are at a higher elevation than LEF landslides, the ‘Massenerhebung’ or mass elevation effect (Grubb 1971) should reduce any
vegetation differences due solely to elevation. Taken together, the similarity in climate, soils and vegetation between MCF and LEF makes this pair of sites appropriate for comparative island/mainland studies.

Predation, disease and germination experiments

At both sites, I hand-collected ripe seeds from 25-30 trees of each test species and examined seed predation, disease and germination both before and after dispersal – which provided more detail into the regeneration biology of the individual species. The following were considered evidence of pre-dispersal seed predation: empty seed/fruit stalks obviously removed by birds or mammals and non-abortive seeds with extensive insect damage either seen with a hand lens or implied by the ability of the seed to float in water (Myster & Pickett 1993). Intact (presumed viable) seeds were taken back to the laboratory, placed on moist paper in plastic-wrap covered petri dishes, and put under plant growth lights (Sylvania 40 watt wide spectrum GRO-LUX) to create a warm, humid environment. This was necessary to determine which non-germinating seeds were lost to fungus and which were non-viable. After one month seeds were examined under a dissecting microscope for germination and fungal growth, and assigned to one of three categories: germinated, diseased or other. Seeds that failed to germinate and had visible fungal damage were classified as ‘diseased’ and seeds that failed to germinate but had no microscopically visible fungal damage were assigned to the ‘other’ category. This categorization is reasonable, though limitations must be kept in mind: germinated seeds with fungal damage had four seeds per dish and Witheringa (0.01) had 10 seeds per dish. Consequently, percentage of seeds remaining in the dishes after placement in a landslide was the dependent response variable instead of raw number of seeds remaining or lost (Myster & Pickett 1993). Neither Puerto Rican nor Costa Rican seeds had passed through a bird gut. Because gut passage did not affect germination success for Phytolacca rivioides, Witheringa solanacea and W. coccoloboides in another MCF experiment (Murray 1988), I assume that any effect of bird gut passage on the results here would be minimal.

The effect of mammal and insect exclusion on post-dispersal seed removal in all landslides was tested using four treatments:

1. cages of 1 cm² mesh hardware cloth enclosing open plastic petri dishes of 9 cm diameter to exclude mammals – including the roof rat Rattus ratus and the mongoose Herpestes mungo in Puerto Rico (Weinbren et al. 1970) and, in Costa Rica, the rodents Peromyscus mexicanus, Heteromys desmarestianus and Orzyzomys albicularis, the variegated squirrel, Sciurus variegatoides, and the agouti, Dasyprocta punctata (Hayes & Laval 1989) and large invertebrates such as the Puerto Rican land crab Epibiopea simpatifrons;

2. tanglefoot (a sticky resin) spread on the inside of petri dishes to exclude small non-flying invertebrates;

3. both treatments on the same petri dish; and

4. a control without any treatment.

For each of the four treatments, seeds of each of the six species were placed on top of local soil spread in separate dishes for a total of 24 dishes. Dishes were then arranged randomly and glued to a wooden platform (0.5 m x 0.5 m; surface area = 0.25 m²). Over the platform, a plastic roof at a height of 0.5 m was placed to protect dishes from the weather and to reduce any seed loss due to rain and wind. Platforms were anchored in place with a 30 cm long plastic stake. Five colored inedible plastic seed mimics of similar shape and mass were placed in each control petri dish to see if any seed losses occurred due solely to rain impact. In addition, extra dishes with seeds but no soil were placed on the Puerto Rican Rio Blancos landslides to determine if soil contact was needed for fungal infection of seeds.

All replicates were placed in the microhabitats of forest border (in the forest just outside the lip where soil and vegetation slid), landslide border (just inside the lip), and center of the landslide on three transects, for a total of nine replicates per landslide. The transects were 20 m apart starting 20 m from the top of the slide. The experiment design was six species (four in Costa Rica) × four treatments × nine replicates. The Puerto Rico experiment ran for 26 days from mid-March to mid-April 1992, and the Costa Rica experiment ran for 24 days in May 1992. At the end of the field experiment
and on the same day, the number of seeds remaining in all dishes was recorded. Then all seeds left in the control dishes were pooled for subsequent incubation, to detect fungal infection and germination, for 60 days in the laboratory either in Puerto Rico or Costa Rica (same protocols as for pre-dispersal seed incubation).

Treatment effects were investigated using nested analysis of variance (ANOVA; Sokal & Rohlf 1981; Anon. 1985) where the dependent variable was percentage of seeds remaining. For species with four seeds per dish, the range of response values was too narrow to approximate a continuous function and so logistic regression analysis was used (Anon. 1985; Myster & Pickett 1993). In both cases, only significant results are given. Nested ANOVA allowed me to partition the variance in seed percentage remaining and identify significant treatment effects. Here, this means groups (sensu Sokal & Rohlf 1981) of dishes pooled in individual microhabitats (e.g. landslide center dishes vs. landslide border dishes vs. forest border dishes, referred to as the within-landslide variance component in the results) vs. groups of dishes pooled in each landslide (e.g. ES2 dishes vs. RB2 dishes, referred to as the among-landslide variance component in the results). Finally, to assess significant differences among seed process mechanisms, sites or pre/post dispersal levels, a simple t-test was used (Sokal & Rohlf 1981).

Results

Puerto Rican seed predation

Because fewer than 1 % of the colored mimic seeds were lost to the weather in either the Puerto Rican or the Costa Rican experiments, significant treatment seed losses were assumed to be due to active removal by animals which leads to predation (Myster & Pickett 1993). In addition, seeds that were obviously eaten but not removed were counted as predation. Both pre- and post-dispersal predation losses were small for all six Puerto Rico species, only once exceeding 10 % (Fig. 1). In addition, post-dispersal predation was greater than pre-dispersal in four of the six test species; Miconia had the only significant increase (3 % pre/15 % post; t = 7.65, df = 2, p = 0.05). There was a trend of increased predation for smaller-seeded species (e.g. Miconia, Cecropia, Gonzalagunia) compared to larger-seeded species (e.g. Ocotea, Palicourea, Phytolacca; but see Uhl 1987).

The only significant treatment effect was for Cecropia schreberiana under the non-volant insect exclusion treatment (Table 1) which reduced predation from 9 % to 2 %. Ants may have been the predators because they were sampled in the five Puerto Rico landslides (Myster in press) and fed on Cecropia seeds when offered seeds from all test species in feeding trials. Most post-dispersal predation occurred in the first week regardless of species and, consequently, the

Fig. 1. The fate of seeds of plant species that colonize landslides in Puerto Rico: eaten by predators (clear), killed by disease (dark-crossed), germinated (light-crossed) or unaffected by these three mechanisms (‘other’ in the Methods; black) both before dispersal (pre) and after (post).
Table 1. Complete ANOVA table for the dependent variable of percentage of seeds remaining in the Puerto Rican predation field experiment. Significant effects are highlighted in bold type and only those species are given. ss = sum of squares; ms = mean squares.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>ss</th>
<th>ms</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cecropia schreberiana</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Insects excluded</td>
<td>1</td>
<td>1.82</td>
<td>1.82</td>
<td>3.45</td>
<td>0.05</td>
</tr>
<tr>
<td>Mammals excluded</td>
<td>1</td>
<td>0.23</td>
<td>0.23</td>
<td>0.50</td>
<td>0.55</td>
</tr>
<tr>
<td>Insects and mammals excluded</td>
<td>1</td>
<td>0.39</td>
<td>0.39</td>
<td>0.67</td>
<td>0.43</td>
</tr>
<tr>
<td>Error</td>
<td>41</td>
<td>31.16</td>
<td>0.76</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

rate of seed loss was approximately 1 - 2 % per day (average of 10 % for all species divided over 7 days), similar to temperate forest disturbance studies in New Jersey, USA (Myster & Pickett 1993). Partitioning the variance for the only species having significant losses (Cecropia) showed 80% variance among the five slides (ANOVA variance component: VC = 0.435), leaving 20 % variance within the five slides (VC = 0.061). Here, as in all Puerto Rican results, among-slide variances were not decreased by grouping landslides into common watersheds even through local hydrology is presumed to be important in recovery from disturbance (Waide & Lugo 1992).

Puerto Rican seed disease

Seeds in dishes that contained soil did not have a greater infection percentage than those in dishes without soil, and so contact with the soil may not be necessary for infection (but see Augspurger & Kelly 1984). Levels of seed loss to pathogens were similar to the small predation losses for four of the six species (22 % loss maximum) with post-dispersal losses greater than pre-dispersal losses for those four species (Fig. 1) (t-values with df = 2 and p = 0.01 for each species) were:

<table>
<thead>
<tr>
<th>Cecropia</th>
<th>10.45</th>
<th>Gonzalezagia</th>
<th>5.21</th>
</tr>
</thead>
<tbody>
<tr>
<td>Miconia</td>
<td>8.87</td>
<td>Phytolaccia</td>
<td>9.02</td>
</tr>
</tbody>
</table>

Alternatively Ocotea and Palicourea showed much greater loss to pathogens (86 % maximum), more pre-dispersal losses compared to post-dispersal; (t-values with df = 2 and p = 0.05):

| Ocotea | 6.35 | Palicourea | 6.98 |

There were much greater seed losses to pathogens than to predators (t-values with df = 2 and p = 0.01):

| Ocotea | t = 15.45 | Palicourea | t = 20.02 |

In addition, Cecropia and Ocotea lost a relatively greater proportion of seeds to pathogens at the forest edge compared to the center of the landslide (21 % vs. 9 %; similar to seedlings in gaps; Augspurger 1984).

When seeds were isolated and incubated, the fungal genus could be identified under the microscope in many cases. A species of Colletotrichum (Melanconiales) grew from dead Palicourea seeds and is known to inhibit germination and cause seed mortality in some species (Tripathi 1974; Ellis et al. 1979). A young Phytolaccia individual that died after germination exhibited watersoaking and softening of the hypocotyl tissues, which are typical symptoms of Pythium damping-off disease (Hering et al. 1987), and a Pythium species was found growing in the affected hypocotyl. Fusarium species (Moniliiales) grew from Phytolaccia, Palicourea and Ocotea seeds, but it is not known if this was the cause of mortality. However, a Fusarium spec. probably contributed to the death of a Cecropia schreberiana seedling which exhibited a pinkish lesion on the hypocotyl and dead feeder-roots, symptoms typical of Fusarium damping-off and root rot (Huang & Kuhlman 1989).

Another fungus in the Moniliiales, belonging to the genus Arthrospernum (Wang 1972), grew from Cecropia schreberiana seeds although this genus is generally saprophytic (D. J. Lodge pers. comm.). Rhizoctonia spec. infected a Cecropia schreberiana seedling and possibly a Phytolaccia seed and is a known seedling pathogen (Sinclair & Backman 1989). In addition, two unidentified fungi that produced rhizomorphs or root-like structures apparently destroyed seeds of Palicouris. The effects of fungi may have been greater than scored because infected seedlings may be more susceptible to other stresses such as drought, and this may thus contribute to seedling mortality later (D. J. Lodge pers. comm.).

Puerto Rican seed germination

Except for the pre-dispersed seeds of Ocotea and Palicourea, the majority of seeds of all six test species germinated both pre-dispersal and post-dispersal (Fig. 1). Because species that were abundant in landslides were used, this result is consistent with Walker & Neris (1993) who also found a close positive correspondence between abundance and germinability in Puerto Rican landslides. With the exception of the small-seeded Cecropia and Miconia, germination either increased or stayed the same after dispersal for all species, suggesting that some seeds that were lost to predators and pathogens before dispersal were viable and could have germinated after dispersal. Gonzalezagia and Palicourea showed the largest percentage of non-viable seeds (between 32 % and 45 %). Comparison between dishes
with and without soil showed that germination percentages were not affected by contact with the soil after dishes were taken back to the laboratory. These laboratory results are probably a measure of potential germination under field conditions (also see Walker & Neris 1993) but species compare to each other in proportions similar to other LEF landslide and rainforest germination studies (Walker & Neris 1993; Everham et al. 1996).

**Table 2.** Complete ANOVA table for the dependent variable of percentage of seeds remaining in the Costa Rican predation field experiment. Significant effects are highlighted in bold type and only those species are given. ss = sum of squares; ms = mean squares.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>ss</th>
<th>ms</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Cecropia polyplebia</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Insects excluded</td>
<td>1</td>
<td>2.01</td>
<td>2.01</td>
<td>7.21</td>
<td>0.01</td>
</tr>
<tr>
<td>Mammals excluded</td>
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<td>0.33</td>
<td>0.33</td>
<td>0.47</td>
<td>0.65</td>
</tr>
<tr>
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<td>0.31</td>
<td>0.31</td>
<td>0.55</td>
<td>0.51</td>
</tr>
<tr>
<td>Error</td>
<td>14</td>
<td>10.08</td>
<td>0.72</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Urera caracasana</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Insects excluded</td>
<td>1</td>
<td>0.25</td>
<td>0.25</td>
<td>4.02</td>
<td>0.05</td>
</tr>
<tr>
<td>Mammals excluded</td>
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<td>0.19</td>
<td>0.19</td>
<td>0.51</td>
<td>0.43</td>
</tr>
<tr>
<td>Insects and mammals excluded</td>
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<td>0.15</td>
<td>0.15</td>
<td>0.49</td>
<td>0.93</td>
</tr>
<tr>
<td>Error</td>
<td>14</td>
<td>11.34</td>
<td>0.81</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Witheringia succulenta</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Insects excluded</td>
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<td>0.09</td>
<td>0.61</td>
<td>0.70</td>
</tr>
<tr>
<td>Mammals excluded</td>
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<td>0.33</td>
<td>4.52</td>
<td>0.05</td>
</tr>
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<td>0.21</td>
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<td>0.54</td>
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<tr>
<td>Error</td>
<td>14</td>
<td>10.92</td>
<td>0.78</td>
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</tr>
</tbody>
</table>

**Costa Rican seed predation**

Both pre- and post-dispersal predation losses were small for all four Costa Rican species, only once exceeding 10% (*Cecropia* pre-dispersal; Fig. 2). In addition, only *Urera* showed significantly more post-dispersal predation than pre-dispersal (*t* = 10.2, df = 2, *p* = 0.01) and predation levels showed no correlation with seed size for the Costa Rican species. Non-volant insect exclusion reduced seed loss significantly for *Cecropia polyplebia* (Table 2; 3% loss in control dishes vs. 0.5% in exclusion dishes on average; also see Murray et al. 1992) where landslide sampling again implicated ants as potential predators (Myster in press). Insect exclusion also reduced seed loss significantly for *Urera* (Table 2; 5% loss in control dishes vs. 1% in exclusion dishes on average). Mammal exclusion reduced seed loss significantly for *Witheringia* (Table 2; 3% loss in control dishes vs. 1% in exclusion dishes; Murray 1988). Again, most post-dispersal predation occurred in the first week regardless of species: approximately 1% per day (Myster & Pickett 1993). Partitioning the variance for the three species with significant losses showed that most of the variance for *Cecropia* was within landslides (72%; VC = 0.211) compared to among landslides (28%; VC = 0.711), with increased predation closer to the forest. Alternatively, for *Urera* and *Witheringia*, most of the variance was among landslides (70%; VC = 0.201; 75%, VC = 0.195; respectively) compared to within landslides (30%, VC = 0.723; 25%, VC = 0.697; respectively).

**Costa Rican seed disease**

Levels of seed loss to pathogens were similar to the small predation losses for three of the four species (5% loss maximum) with little difference between pre- and post-dispersal (Fig. 2). The exception was small-seeded *Cecropia* which showed large losses of seeds to pathogens, an increase in percentage of seeds lost to pathogens after dispersal (27% pre / 37% post; *t* = 5.23, df = 2, *p* = 0.05) and much greater seed losses to pathogens than predators (*t* = 6.66, df = 2, *p* = 0.05). Individual fungal species could not be identified in Costa Rica.

**Costa Rican seed germination**

Whereas most *Urera* (both pre- and post-dispersal) and post-dispersal *Witheringia* seeds germinated, the other seeds mainly suffered other fates (Fig. 2). No seed mass trends were seen; for example, the small-seeded *Urera* had total pre-dispersal germination and 80% post-dispersal germination (*Urera baccifera* ger-
TOTAL SEEDS

Fig. 3. Combining the results of all plant species of Figs. 1 and 2 into mean percent loss of seeds to predation, disease, germination and ‘other’ of all Puerto Rican plant species and of all Costa Rican plant species both pre- and post-dispersal using the same shading indicators as Fig. 1.

At 14% in a Puerto Rican landslide study; Walker & Neris (1993) with the relatively large-seeded Witheringia germination increasing dramatically after dispersal (Murray 1988). The proportion of total seeds that were non-viable showed large species variation, e.g. Ureña with small percentages and Witheringia with large percentages. Perhaps some of these could have been dormant and still viable, e.g. Cecropia spp. and Witheringia (Murray 1988) can have a long dormancy period.

Puerto Rican vs. Costa Rican seed processes

Comparing the results from Puerto Rico and from Costa Rica (Fig. 3) reveals these similarities: (1) the level of both pre-dispersal and post-dispersal seed predation is low in both sites, (2) germination levels are similar when species are combined and increase after dispersal at both sites, and (3) non-viable seeds are in the 10 - 20% range of total seeds and decrease in percentage after dispersal. By contrast, even though more seeds are lost from pathogens than from predation at both sites, this trend is only significant in Puerto Rico (t = 6.33, df = 2, p = 0.05). For the two plant genera used at both sites, insect predation reduced Cecropia seeds significantly at both sites (the loss of Azteca or other ant species association in Puerto Rico did not seem to affect insect predation levels; Putz & Holbrook 1988) with significantly more Cecropia seeds germinated in Puerto Rico compared to Costa Rica (t = 5.29, df = 2, p = 0.05) and Gonzalagunia had no significant predation at either site, with similar levels of predation and pathogens in Puerto Rico and Costa Rica.

Discussion

Plant species had individualistic (Myster & Pickett 1988) predation, disease and germination responses (Myster & Pickett 1993) and this species variation dominated over seed process, site, and pre/post dispersal differences. Because germination levels are a function of the seeds which escape predation and pathogens, these three regeneration processes are not mutually exclusive and, furthermore, may have probabilistic (e.g. influenced by animal behavior) or stochastic (e.g. fungi dispersal) interactions. In addition the use of plant characteristics to predict seed losses had mixed support. For example there was weak positive correspondence between seed mass and level of predation and pathogens (Louda & Zedler 1985; Uhl 1987), but there may be more support for this hypothesis when the predators are vertebrates rather than invertebrates (Myster & Pickett 1993). Similar to seedlings (Augspurger & Kelly 1984), the vulnerability of seeds to pathogens varies among neotropical species but seed mass is not a good predictor of vulnerability to pathogens (Augspurger 1984) even though light-seeded early successional species may be more susceptible to seedling pathogens than later successional species (Augspurger & Kelly 1984). In general, little is known about what seed characteristics permit or encourage seed infection.

Although higher levels of predation than found in this study have been suggested for Cecropia and Palicourea in other LIF studies (Weinbren et al. 1970), Walker & Neris (1993) found in landslides similar levels to mine and agree that Phytolacca and Gonzalagunia are successful germinators and Palicourea is relatively unsuccessful. Microsite germination cues (light increasing rates but litter, high soil moisture and high temperatures decreasing rates) were shown in a LIF gap study by Everham et al. (1996) suggesting that the small number of moderate temperature microsites in landslides (Myster & Fernández 1995) could be contributing to slow invasion and establishment rates on landslides. Finally, combining the results with other landslide studies shows relationships between seed processes and establishment patterns. Using permanent plot data on LIF landslides which included those used in this study (Myster & Walker in press), there is a positive correspondence between stem density and seed process results seen here; those species with small losses
to predation and disease and large germination levels were common in permanent plots. This pattern held true for some species (Cecropia, Gonolalugina) but not for others (Ureru) in MCF landslides (Myster 1993b).

Species interactions on islands — e.g. seed predation (Janzen 1971) — have been thought to be relatively weak (Janzen 1973) compared to the mainland. However, experimental studies on islands have shown that insect seed predation can be intense (Louda & Zedler 1985). Perhaps surprisingly, this study showed similar levels of all three seed processes (predation, disease, germination) on a neotropical island site and neotropical mainland site with similar life-zone, climate, and flora. The biggest difference between the Puerto Rican ecosystem and the Costa Rican ecosystem may be the lack of native terrestrial mammals in Puerto Rico (Nilsson et al. 1985), which could lead to a lack of mammal-dispersed plant species and allow other animal species to move up in the island food chain to replace the mammals (as in Puerto Rico; Waide 1987). Taken together, the results suggest that islands and the mainland may not differ in much more than basic climate or species composition (here mammal; Lugo 1987) and, consequently, run counter to the model of reduced strength of biotic processes (e.g. competition, predation, herbivory) on island ecosystems compared to mainland ecosystems (Janzen 1973).

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