Landslides cause spatial and temporal gradients at multiple scales in the Luquillo Mountains of Puerto Rico

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Landslides represent one of the most severe disturbances in montane forests because the main consequence of their occurrence is loss or downslope redistribution of the majority of the above- and below-ground biomass. We examined among-landslide gradients (size, slope, aspect, age, elevation) on 142 landslides in the Luquillo Mountains, Puerto Rico, created by three storms in 2003–2004. We also examined within-landslide gradients (top to bottom, edge to center, successional development) by reviewing 20 yr of landslide data in the Luquillo Mountains. Landslide abundance and plant successional patterns do not closely reflect the elevation gradient that is characteristic of this mountain range, unlike many abiotic and biotic factors that do. Numerous physical gradients resulting from landslides, including soil nutrients, slope, age, and distance to edges and the base of a landslide, strongly influence colonization, growth, and survival of vegetation in the Luquillo Mountains. However, some gradients appear more pronounced than others, and the influence of each gradient on landslide recovery likely depends on both biotic responses to the net effects of multiple, overlapping interactions among gradients (e.g. soil slope and fertility) and the temporal and spatial scale at which attributes are measured. Therefore, even when the many gradients that influence plant colonization and landslide development are known, accurate predictions of species composition and time to forest recovery remain challenging.

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Ecological gradients result from variation in organisms and their environments and often occur across a wide range of spatial (microsites to landscapes) and temporal (minutes to millennia) scales. Some ecological gradients such as elevation derive from climatic and topographical conditions, while others result from disturbances. Disturbances can be a key component in the formation of gradients because they cause spatially uneven losses of biomass that result in changes to both environmental conditions (e.g. temperature, light, soil properties) and resident biota (Pickett and White 1985, Walker in press). The uneven damage caused by disturbances can be usefully exploited as a natural experiment to understand the relative influences that such abiotic variables as elevation, light conditions, soil fertility, or soil stability have on the temporal gradient of community development following a disturbance (succession; Tilman 1988, McDonnell and Pickett 1993, Dale et al. 2001, Walker and del Moral 2003). Biotic responses to disturbances are complex and are influenced by the severity of a disturbance and resultant spatial heterogeneity of

resources as well as by the life cycles and interactions of the species themselves. Gradients provide a useful mechanism to analyze the contributions of many interacting abiotic and biotic factors along spatial (e.g. elevation) and temporal (e.g. seasonality or succession) scales (Gentry 1988, Hall et al. 1992, Dickson and Foster 2008). Typical gradients created by landslides in tropical forests include light levels, slope, soil fertility and stability, and vegetative cover.

Landslides are common disturbances in mountainous regions in both temperate and tropical environments; they are triggered by high rainfall events, earthquakes, or human land-use practices such as road construction, logging, drilling, and mining (Adams and Sidle 1987, Larsen and Torres-Sánchez 1998, Sidle and Ochiai 2006). Landslides are among the most severe of all disturbances based on the amount of biomass lost per unit area, and their occurrence results in both landscape- and local-scale gradients of physical and biological attributes (Guariguata 1990, Walker et al. 1996a, Shiels et al. 2006). Landslides contribute to habitat patchiness (i.e. abrupt or discontinuous

gradients) within a given mountainscape (Geertsema and Pojar 2007). Landslides of different sizes, shapes, and locations are often at various states of succession and species composition (Garwood et al. 1979). Such habitat heterogeneity created by landslides can provide refugia for numerous species to complete parts or all of their life-cycles (Dalling 1994, Kessler 1999, Restrepo et al. 2009). Additionally, gradients of physical conditions are common within individual landslides and affect a wide range of plants, animals, microbes, and most ecosystem functions such as decomposition, primary productivity, and nutrient and hydrologic cycles.

Not all gradients result in changes in species composition, abundances, and/or ecosystem processes, suggesting that multiple factors may be at play when comparisons are made across gradients. While many plant species are unique to particular elevations, forest types, and successional states (Vásquez and Givnish 1998, Gould et al. 2006), some plant species within a given mountain range are commonly found across forest types, as shown for several trees in the Luquillo Mountains of Puerto Rico (Lash-Marshall et al. 2013), as well as across a variety of landslide ages and elevations (Miles and Swanson 1986, Guariguata 1990, Dalling 1994). For example, *Pseudotsuga menziesii* and *Rubus ursinus* were present on 23 of 25 landslides of ages 6–28 yr that were studied at elevations 460–1100 m in the Cascade Mountains of western Oregon (Miles and Swanson 1986). All 20 landslides (1–52 yr since landslide disturbance) studied by Guariguata (1990) at elevations 530–880 m in the Luquillo Mountains of Puerto Rico were colonized by both *Cecropia schreberiana* (previously *C. peltata*) and *Prestoea acuminata* (previously *P. montana*). Dalling (1994) found that all seven landslides (aged 15 to more than 50 yr since landslide disturbance) at elevations 1440–1780 m in the Blue Mountains of Jamaica were colonized by *Clethra occidentalis*. Some aspects that commonly influence species presence or community composition across gradients include: physiological tolerances, resistance and resilience to disturbance, ability to successfully reproduce and disperse, and ability to coexist with additional species (Grubb 1986, Bruijnzeel and Veneklaas 1998, Vásquez and Givnish 1998). Isolating particular mechanisms of species distributional changes along gradients are complicated by the interactions among many of these variables.

Landslides represent one of the most intriguing disturbances to study in association with gradients because of the wide range of gradient types and scales both within landslides and in the landscape where landslides typically occur (e.g. montane ecosystems). Here we review the types of gradients associated with landslides in the Luquillo Mountains of Puerto Rico. We focus on gradients that exist among landslides within a population (i.e. landscape gradients, and those landslides triggered simultaneously from a single storm), the relationship between the prominent elevation gradient and landslide abundance, and within landslide gradients that are created by landslides.

We also discuss the influence of these gradients on plant succession.

Study site

The Luquillo Mountains in northeastern Puerto Rico (18°18′N, 65°50′W) includes the Luquillo Experimental Forest (LEF), an 11000 ha forest that spans elevations 100 to 1075 m. Mean annual precipitation increases with elevation from approximately 2300 mm at 100 m to 3600 mm at 1051 m (Brown et al. 1983). Temperatures average 4.5°C lower at the top of the mountain range (ca 1000 m) compared to temperatures (mean monthly is 21–25°C) at the weather station at 350 m (Brown et al. 1983). The Luquillo Mountains are commonly described by their four forest types that are separated by elevation. The tabonuco *Dacryodes excelsa* forest (subtropical wet forest in Holdridge System, Ewel and Whitmore 1973) dominates below ca 600 m elevation. Above ca 600 m is a subtropical rain forest characterized by palo colorado *Cyrilla racemiflora* trees, while above ca 950 m a dwarf forest occurs and *Tabebuia rigida* and *Ocotea spathulata* are dominant trees. Nearly monotypic forest stands of palm (*Prestoea acuminata*) are interspersed throughout all vegetation types in areas of poorly drained soils (Waide and Lugo 1992). Plants that typically colonize the high-light environments found on most LEF landslides include several types of grasses (e.g. *Andropogon* spp., *Paspalum* spp.), thicket-forming ferns (*Gleichenella pectinata*, *Sticherus bifidus*), treeferns (*Cyathea* spp.), and woody colonizers such as *Cecropia schreberiana*, *Prestoea acuminata*, *Miconia* spp., *Piper* spp., and *Psychotria* spp. (Guariguata 1990, Myster and Walker 1997, Shiels and Walker 2003).

Soils derived from volcaniclastic parent material (Ultisols; Cretaceous tuffaceous sandstone and siltstone weathered from extrusive bedrock; hereafter volcaniclastic soils) dominate the mountain range, whereas soils in parts of the upper elevations may be underlain by those derived from quartz-diorite bedrock (Inceptisols; weathered from intrusive bedrock; hereafter dioritic soils; Seiders 1971, Larsen et al. 1998). Landslides that occur on these two types of geologic substrates have distinct features, such as different soil and vegetation characteristics (Table 1, Shiels et al. 2008, Walker and Shiels 2008). Landslides in the Luquillo Mountains are generally a result of high rainfall events and are shallow soil slips, debris flows, and slumps (Larsen and Torres-Sánchez 1996).

Gradients among landslides in the Luquillo Mountains

Variation in landslide size, abundance, and location has important consequences for landscape patchiness. The forest gaps that result from landslides can range in size from

Table 1. Characteristics of landslides occurring on the two types of parent materials (geologic substrates) in the Luquillo Mountains, Puerto Rico. For vegetation comparisons, the litterfall inputs into landslides are largely from the surrounding edges (i.e. intact forest), and the comparison for aboveground colonization is for rate, including biomass and cover. All comparisons are based on data from Shiels et al. (2008) and Walker and Shiels (2008) where 30 landslides (each ca 1 yr old) were compared.

	Volcaniclastic	Quartz-diorite
Elevation	Low, Medium, High	High
Age of parent material	Old	Young
Soil		
Dominant particle size	Clay	Sand
Water-holding capacity	High	Low
Total nitrogen	High	Low
Erosion rate	Low	High
Vegetation		
Litterfall inputs	High	Low
Aboveground colonization	High	Low

those equivalent to small treefalls (< 12 m², Shiels et al. 2008) to those comparable to entire watersheds (11 km², Velázquez and Gómez-Sal 2007). Factors that commonly trigger landslides include the direction of prominent weather patterns (Larsen and Simon 1993, Larsen and Torres-Sánchez 1996), proximity to roads (Swanson and Dyrness 1975, Guariguata and Larsen 1990, Larsen and Torres-Sánchez 1998, Jones et al. 2000), and the steepness of hillslope (Sidle and Ochiai 2006). There is a wide range of landslide sizes that are found in different topographical settings that can influence the patterns of vegetation colonization and structure (Walker et al. 1996a, Myster et al. 1997). The gradient of landslide succession begins where bare soil dominates recent landslides, and extends to where the vegetation community resembles the pre-landslide conditions of a late-successional forest. Thus, landslide gradients occur across the landscape as a result of the large range of landslide sizes, aspects, slopes, and ages since a previous landslide.

Frequent storms that occur in the Luquillo Mountains result in flooding and numerous landslides. On average, 1.2 storms yr⁻¹ produce landslides in the Luquillo Mountains (Larsen and Simon 1993) and approximately half of the landslides occur near roads (Guariguata and Larsen 1990, Larsen and Torres-Sánchez 1996). Such storms provide the opportunity to examine landslide variability across this mountain range. During 2003–2004, there were three significant storms (April 2003, November 2003, and September 2004) that each produced 200–600 mm of rainfall in 24 h and each triggered more than 30 landslides. We counted landslides that occurred following each of the three storms by driving all major roads in the LEF (route/road: 186, 930, 966, 988, and 191 except for the southern portion below 600 m; Fig. 1) and walking established trails while visually scanning the forest for

landslides triggered by each storm. We estimate that ca 50% of the LEF was visually covered by our survey. We defined landslides as a discrete event in time resulting in the downslope mass movement of the topsoil layer of the soil profile (at least the O- and A-horizons), and we only counted landslides with ≥ 12 m² of bare soil/substrate. Size, aspect, and elevation of all landslides were estimated; slope was measured on a subset of the landslides (n = 30, included in Shiels et al. 2008) in the April 2003 storm and all landslides triggered by the November 2003 and September 2004 storms.
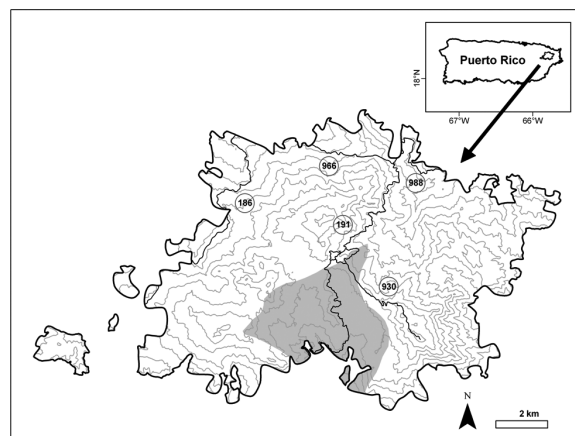

Figure 1. Map of the Luquillo Experimental Forest in the Luquillo Mountains, northeastern Puerto Rico, showing the major roadways used in the census of 142 landslides during 2003–2004 as well as the two dominant soil types. The shaded region represents dioritic soils whereas the unshaded (white) region represents volcaniclastic soils. Contour lines are at 100 m intervals where the lowest contour line is 100 m and the highest is 1000 m.

We recorded 142 landslides in the LEF originating from the three storms, and the sizes of the majority of the landslides following each of the three storms were ≤ 100 m² (Fig. 2A). Few landslides were > 300 m² and the two largest landslides were 1175 m² (April 2003) and 1375 m² (September 2004), the latter causing temporary road closures. Each of the three storms produced a size gradient of landslides with the same general frequency distribution, resulting in a landscape mosaic fragmented mainly by numerous, small-sized landslides. The majority of the 46 landslides at 530–850 m elevation in the Luquillo Mountains that were observed and measured by Guariguata (1990) using aerial photographs from 1936 to 1988 were ≤ 400 m² and the size class with the most landslides (40%) was 200–400 m². By contrast, > 99% of all landslides triggered by the three storms in 2003–2004 were < 400 m². The large difference in landslide abundance between these two studies may be explained by the smaller elevation range measured by Guariguata (1990), and the exclusion of small landslides (especially those < 60 m²) by Guariguata (1990) that were obscured by adjacent vegetation during aerial photographic analysis.

Slope is a critical factor determining landslide formation, and despite the wide-range of slopes on which landslide disturbance typically occurs (20–90°, Sidle and Ochiai 2006), slopes and landslides in the Luquillo Mountains are rarely > 45° (Guariguata and Larsen 1990). Slope is also one of the most important attributes contributing to rates of colonization and vegetation development on landslides (see section on Gradients within landslides in the Luquillo Mountains, Guariguata 1990, Walker et al. 1996a). All landslides from the three storms had slopes ≥ 21° and most had 26–45° slopes (Fig. 2B). Similarly, > 70% of the landslides identified from 1936–1988 aerial photographs by Guariguata (1990) were on 30–40° slopes. Landslide studies outside Puerto Rico had steeper or comparable slopes to those triggered by the three storms in 2003–2004; the slopes of the 25 landslides studied by Miles and Swanson (1986) in the Cascade Mountains of Oregon were 22–60°, and the seven landslides studied by Dalling (1994) had slopes of 40–50°. Although the loss of soil and rock associated with landslides can alter the natural slope of a hillside, the difference between pre- and post-landslide slope is typically subtle and depends on the depth of soil and debris deposition at the base of a landslide. The gradient of slopes upon which landslides in the Luquillo Mountains occurred during our surveys were those ≥ 21°, which is a steeper cut-off than the > 12° slopes that Larsen and Torres-Sánchez (1998) proposed for Puerto Rican ecosystems that are more heavily dominated by anthropo-
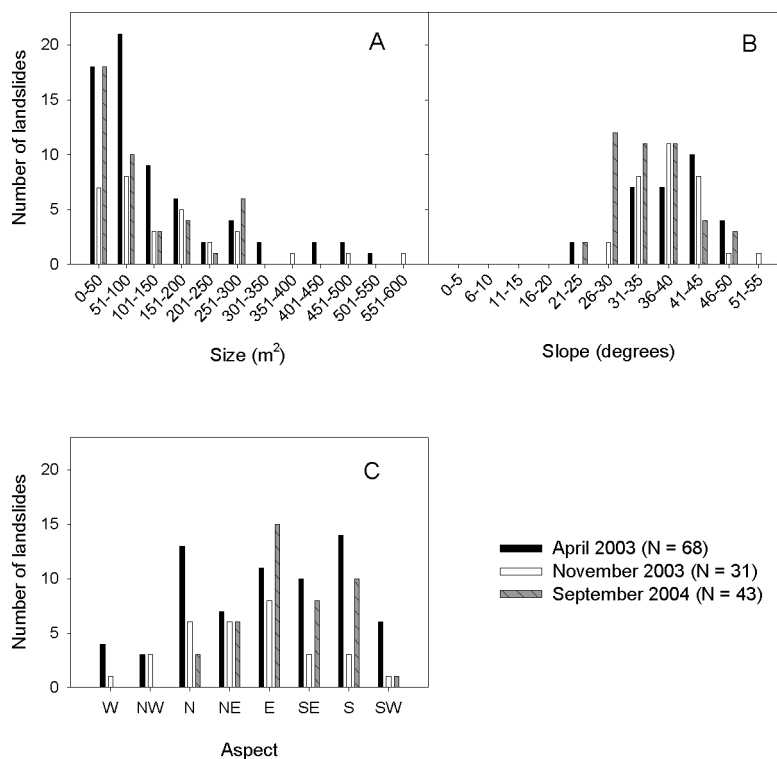

Figure 2. Landslides in the Luquillo Mountains triggered by three major storm events (2003–2004) and arranged by (A) size, (B) slope, and (C) aspect. Two large landslides are not shown here; one was from the April 2003 storm that was 1175 m² and one was from the September 2004 storm that was 1375 m². Only 30 of the 68 landslides following the April 2003 storm were measured for slope.

genic disturbance (e.g. roads, structures, agriculture). This discrepancy highlights the destabilizing effect that human land use has on slopes (Swanson and Dyrness 1975, Jones et al. 2000).

The aspect (direction) in which landslides occurred following the three storms was wide-ranging but landslides facing west (or NW or SW) were least common (Fig. 2C). Because the prevailing weather patterns and storms affecting Puerto Rico are usually from the northeast (Weaver 1991, Larsen and Torres-Sánchez 1998), it was expected that west-facing slopes would have fewer landslides. The April 2003 storm triggered landslides across a wide spectrum of aspects, including those facing north, east, and south. During the November 2003 and the September 2004 storms, most landslides occurred on east-facing slopes (Fig. 2C), further highlighting the variation in physical aspects of landslides that result from different storm events. The 16 landslides studied by Myster and Walker (1997) in the Luquillo Mountains had most aspects represented except for south-facing slopes; only north to west landslides were studied by Walker (1994), and only northwest to east landslides were studied by Shiels and Walker (2003) and Shiels et al. (2006). Not only do landslides appear to be less common on west- and south-facing slopes in the Luquillo Mountains, but Myster et al. (1997) found that the structural complexity of the landslide vegetation was greater on landslides that faced away from the dominant wind direction of most recent hurricanes (i.e. southeast-facing), which further indicates the link between physical attributes of landslides and vegetation development.

The degree to which landslides are clustered across the mountainscape further contributes to landscape patchiness. The April 2003 storm triggered 6.1 landslides km^{-1} along the first 1.8 km of Route 930, 2.1 landslides km^{-1} along Route 988, and only 0.3 landslides km^{-1} along Route 186. A possible explanation for this discrepancy includes less rainfall from the storm occurring on the western side of the mountain range; El Verde station on the western side had 235 mm, whereas Sabana station on the eastern side had 474 mm (Luquillo Meteorology 2011). Additionally, the volcaniclastic soils on Routes 186 and 988 are less susceptible to erosion compared to dioritic soils that underlie the lower portion of Route 930 (Table 1, Guariguata 1990).

Landslide age is a key characteristic of patch structure because a given section of the landscape can have landslides in multiple stages of succession (Geertsema and Pojar 2007). Most assessments of landslide age use aerial photographs (Guariguata 1990, Zarin and Johnson 1995a, b, Myster et al. 1997) and field documentation (Miles and Swanson 1986, Fetcher et al. 1996, Walker et al. 2010); although in ecosystems with strong seasonality, tree-rings are also used to establish when a given landslide occurred (Grau et al. 2003, Blodgett and Isacks 2007). Re-sliding, which is when a second landslide occurs over a previous one, can be common in areas prone to landslides such as

in Tanzania where six out of fourteen landslides experienced re-sliding within seven years of each initial landslide (Lundgren 1978). Because landslides result in the loss of the majority of vegetation cover and organically-rich topsoil, there is little remaining substrate and biota to absorb water and anchor soils (Sidle et al. 2006). Therefore, heavy rains on relatively bare landslides can cause sediment loss from the landslide surface (Lundgren 1978, Dalling and Tanner 1995, Larsen et al. 1998, Walker and Shiels 2008), or more severely, cause a second landslide. Using identical methods and survey locations during 2003–2004 enabled us to quantify re-sliding for those landslides triggered by the November 2003 and September 2004 storms. Age estimates of surfaces where landslides occurred were based on past landslide documentation and research plots.

Nearly half of the landslides occurring in November 2003 were on < 1 yr old landslides (i.e. the April 2003 landslides), whereas the majority of the remaining landslides in November 2003 occurred on older substrates that had not experienced a landslide in ≥ 15 yr (Fig. 3). Similarly, approximately half of the landslides in the September 2004 storm occurred on < 1 yr old landslides (i.e. the November 2003 landslides) or 1–2 yr old landslides (i.e. the April 2003 landslides), where the majority of the remaining landslides triggered in September 2004 occurred on substrates ≥ 15 yr old (Fig. 3). The apparent bimodal distribution of substrate ages where re-sliding occurred may be the result of vegetation interception and soil and rooting depth. Landslides initially have little vegetation cover, and therefore the abundance of bare soil on the youngest substrates probably enhances subsequent erosion. The intermediate-aged surfaces are typically covered with low-statured vegetation that intercepts and diverts precipitation and also has dense but shallow root structure that may retard subsequent landslides. The oldest (> 15 yr)
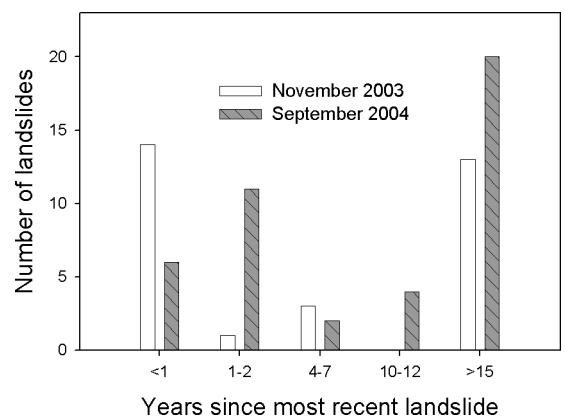

Figure 3. Incidence of re-sliding (a landslide occurring over a previous landslide) on different aged surfaces in the Luquillo Mountains, Puerto Rico, when measured after storm events that triggered landslides in November 2003 (n = 31) and September 2004 (n = 43).

substrates are probably the most common in the Luquillo Mountains and their relatively well-developed soils experience deeper rooting and taller aboveground biomass than vegetation on younger landslides, thereby both intercepting and diverting water until a critical threshold results and triggers a landslide (Larsen and Simon 1993). Although several studies in the Luquillo Mountains purposely chose landslides of varying ages for study (e.g. landslide ages to ca 50 yr old in Guariguata 1990, and Zarin and Johnson 1995a, b), we know of no previous quantification in this mountain range of the frequency of re-sliding, or the ages of the surfaces affected by re-sliding. Landslides in the Luquillo Mountains are dynamic disturbances that occur on a variety of different aged substrates where re-sliding can be common and such subsequent erosion can alter plant successional processes. Additional heterogeneity in landslide size, slope, aspect, and clustering results in multi-faceted gradients of physical conditions that contribute to the landscape mosaic.

Minimal effects of the elevation gradient on landslide abundance and vegetation recovery

The elevation gradient in the Luquillo Mountains has been the focus of much past research that mostly includes changes in abiotic factors such as soil properties (Silver et al. 1999, McGroddy and Silver 2000), temperature, and rainfall (Brown et al. 1983), as well as studies relating these abiotic factors that are coincidental with elevation variation to changes in patterns of plant (Weaver 1991, 2000, Walker et al. 1996b, Waide et al. 1998, Gould et al. 2006, Barone et al. 2008) and animal (Richardson et al. 2005, González et al. 2007) communities. During the three storm events in 2003–2004, landslides occurred across the elevation gradient except for the mountain peaks > 900 m but did not form a close association with elevation ($p > 0.05$, $R^2 = 0.02$) even when adjusting for land area ($p > 0.05$, $R^2 = 0.03$, Fig. 4). Above 900 m the vegetation is comprised mostly of dwarf forests that may be better adapted to withstand high rainfall and landsliding (Walker et al. 1996b); the presence of exposed rock peaks and areas of modest slopes may be additional factors that contribute to the low frequency of landslides at the uppermost elevations. The majority of landslides following each of the three storms occurred between 600 and 900 m elevation, which is the elevation range that is commonly underlain by dioritic soils. Although relatively few landslides > 600 m elevation were on volcaniclastic surfaces (11 in April 2003, five in November 2003, and 10 in September 2004), all of the landslides that occurred below 600 m elevation were on volcaniclastic soils. Because elevation is confounded by soil type in the Luquillo Mountains (i.e. dioritic soils are only at upper elevations; Fig. 1), it is difficult to isolate the effect of elevation on landslides or other soil-dependent proc-
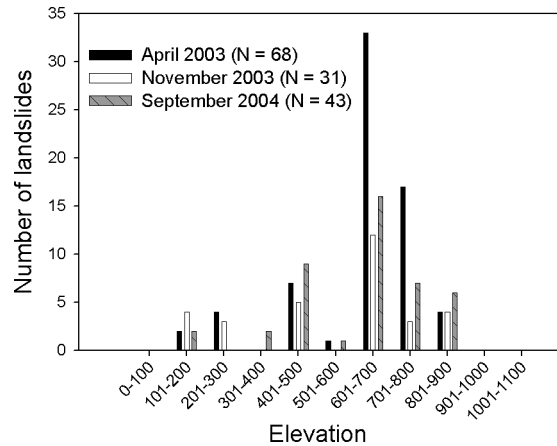

Figure 4. Elevations (above sea level) of landslides in the Luquillo Mountains that were triggered by three major storm events (2003–2004). Approximately 80% of the surface area of the Luquillo Mountains occurs at 200–800 m elevation, whereas ca 5% occurs at < 200 m and ca 15% occurs at > 800 m.

esses and attributes (Shiels et al. 2008, Walker and Shiels 2008). When landslides at all elevations were considered for each of the three storms, 37, 58, and 56% of landslides occurred on volcaniclastic soils in April 2003, November 2003, and September 2004, respectively. Guariguata (1990) used aerial photography to determine the amount of area affected by landslides from 1936–1988 in the Luquillo Mountains, and found that the total aerial coverage of landslides occurring on dioritic substrates was nearly twice that of those occurring on volcaniclastic substrates. Of the 46 landslides identified by Guariguata (1990), 37 (or 80%) were on dioritic soils, which constitute a greater proportion than the number of landslides that occurred on dioritic soils between 2003 and 2004 (75 of 142, or 53%). However, Guariguata (1990) only identified landslides > 60 m² that occurred in the dioritic-rich elevations of 530–850 m. When the comparable landslide size and elevation characteristics used by Guariguata (1990) were applied to the 2003–2004 storms, 47 of 68 (69%) of the landslides occurred on dioritic soils. Rather than reflecting a clear elevation pattern, it is more likely that landslide abundance in the Luquillo Mountains is influenced by multiple factors that may include abiotic correlates of elevation (e.g. rainfall) but are more heavily influenced by soil type (Table 1).

Few landslide studies have examined plant succession along the elevation gradient in the Luquillo Mountains. With soil type confounded by elevation, and few landslides occurring on volcaniclastic soils > 600 m, the conclusions about vegetation changes with respect to elevation are challenging. However, through ordination analyses using at least 30 landslides that spanned the elevation gradient in the Luquillo Mountains, both Myster et al. (1997) and Shiels et al. (2008) found that soil type (volcaniclastic

vs dioritic) explained more variation and better predicted differences in vegetation development (biomass and structure) than did elevation. The absence of a close association between elevation and the landslide plant community was also found on a single large landslide spanning elevation 170–1150 m in Nicaragua (Velázquez and Gómez-Sal 2007). There is clearly a need for more examination of plant succession across elevational gradients, both in the Luquillo Mountains and elsewhere.

Gradients within landslides in the Luquillo Mountains

Strong gradients exist within landslides in the Luquillo Mountains that affect patterns of plant colonization and succession (Guariguata 1990, Myster and Fernández 1995, Walker et al. 1996a, Shiels et al. 2006). Landslides create a number of vertical (top to bottom) and horizontal (edge to center) gradients, as well as more abrupt or discontinuous gradients (i.e. patches) largely resulting from forest fragments (rafts or 'islands') that were resistant to landsliding (Fig. 5). During the last 20 yr, more studies in the Luquillo Mountains have focused on the spatial gradients within individual landslides than gradients among landslides.
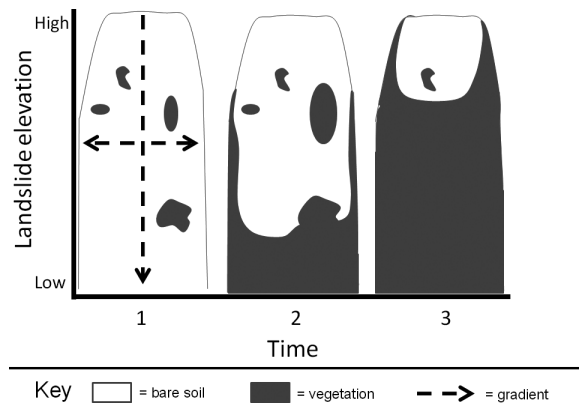

Figure 5. Diagram of the prominent spatial gradients within landslides and their association with patterns of vegetation recovery. Two of the gradient types (top to bottom, and center to edge) are shown with dashed arrows in time period 1, and the vegetation ovals and polygons represent remnant forest patches, which are abrupt and discontinuous gradients. The direction of the dashed arrows correspond to increasing amounts of soil organic matter, viable seeds, and rates of plant colonization and cover. Vegetation recovery occurs fastest at the landslide base (deposition zone) and at the forest edge. Remnant patches can grow and expand, break apart and shrink (by subsequent erosion), or remain unchanged. Not shown are the possible post-landslide inputs of organic matter from sloughing and litterfall from the forest edge. Based on observations in the Luquillo Mountains, it may take an average of ca 5 yr (volcaniclastic soils) to ca 40 yr (dioritic soils) for vegetation to resemble time period 3.

The downslope movement of material coincidental with landsliding produces distinct zones along the vertical gradient of a landslide (Restrepo et al. 2009). The initial failure zone, commonly called the slip face, is the zone where vegetation and soil are initially removed and transported downslope. The slip face generally has the steepest slope, and commonly takes the longest for vegetation to colonize (Adams and Sidle 1987, Guariguata 1990, Elias and Dias 2009). The deposition zone is at the base of the landslide where most of the material transported from the slip face resides. The deposition zone is much less steep relative to the slip face, and it is typically a conglomerate of surface and deeper soils, rocks, vegetation, and organic matter at various states of decomposition (Flaccus 1959, Adams and Sidle 1987). Road-related landslides often have their deposition zones removed in order to clear roadways (Shiels et al. 2008). Many landslides have a third zone, the chute, found between the slip face and deposition zone. The chute is a transport zone for the initial material from the slip face as well as an area where additional material can be scoured. The chute is often the longest zone on a landslide, such as the 3 km-long landslide that occurred in Nicaragua (Velázquez and Gómez-Sal 2007), but on very small landslides (e.g. < 12 m² in the Luquillo Mountains) the chute zone is not always present or identifiable.

Abiotic and biotic characteristics reflect the spatial and physical differences among landslide zones in the Luquillo Mountains. By comparing the upper (slip-face and upper portion of the chute) and lower (deposition) zones of eight recent (< 1 yr old) landslides, Guariguata (1990) found there was much higher soil fertility in the lower zone relative to the upper zone, which included an 8-fold increase in soil organic matter, or carbon (C), a 4-fold increase in soil potassium (K), and a 3-fold increase in total soil nitrogen (N). In a similar comparison using slightly older (5–6 yr) landslides, Li et al. (2005) found that soil C was ca 2-fold higher in the lower zone than the upper zone. Biotic differences on landslides in the Luquillo Mountains often correlate with the soil fertility gradient from upper to lower portions of the landslide. For example, Guariguata (1990) found that seedlings were 4–18 times more abundant in the lower landslide zone relative to the upper zone, and that although seeds were absent from the soil seed bank in the upper zone there were at least four species of viable seeds in the lower zone soils. The abundance of earthworms and soil microbes (particularly fungi) were also correlated with enriched soil C in the lower zone (Li et al. 2005). Additional comparisons between these two landslide zones made on older landslides (2–52 yr old) indicated that tree density and growth were more vigorous in the lower zone than the upper zone (Guariguata 1990). Although light availability (photosynthetic photon flux density, or PPFD) was greater in the upper zone than in the lower zone in a 6-yr-old and 20-yr-old landslide (Fernández and Myster 1995), the enhanced vegetation growth in the lower zone of the landslide is more likely due to the less

steep slope, presence of a viable seed bank, and enhanced soil N and organic matter (Guariguata 1990, Fetcher et al. 1996, Walker et al. 1996a). Therefore, a gradient of soil fertility, soil decomposers, and plant recovery exists on landslides that reflect vertical spatial variation.

A second prominent gradient within each landslide extends perpendicular to the direction of the slope from the forest edge to the center of the landslide (Fig. 5). The edge-to-center gradient has been proposed as the strongest gradient for many abiotic and biotic attributes within landslides (Myster and Fernández 1995). Like the vertical gradient, the edge-to-center gradient is generally most pronounced on young landslides that are in early stages of succession. Beyond the edge of the landslide, the presence of intact forest provides refugia for plants and animals, shade, and a source of organic matter and relatively nutrient-rich soils that can influence colonization of adjacent landslides.

Through studies of relatively large landslides (>1500 m²), abiotic variables strongly change (e.g. 20-fold for photosynthetic photo flux density or PPFD) along the edge-to-center gradient. PPFD increases toward the center of the landslide, as evidenced by one landslide in the Luquillo Mountains where mean total daily values were 0.8, 3.9, 17.3, and 21.6 mol m⁻² for forest, forest border, landslide border, and landslide center, respectively (Fernández and Myster 1995, Myster and Fernández 1995). Similarly, Fetcher et al. (1996) found that canopy openness and light was significantly higher in the center of a 1.5-yr-old landslide relative to the landslide edge. On a 10-yr-old landslide in the Luquillo Mountains, Myster and Schaefer (2003) found that maximum temperature was highest and minimum temperature lowest in the center of the landslide when compared to the edge and forest. Due to the reduced canopy in the landslide center relative to the edge and forest, precipitation measured at 1.5 m above ground for 16 weeks was highest in the center (1390 mm), intermediate at the edge (970 mm), and lowest in the forest (830 mm, Myster and Schaefer 2003). Soil differences are generally less pronounced along the edge-to-center gradient. However, Fetcher et al. (1996) reported that soil moisture and soil C were significantly higher at the landslide edge than at the center. In contrast, Myster and Fernández (1995) did not detect differences in soil moisture, total C, or total N when the edge-to-center gradient was compared, and Myster and Schaefer (2003) found that leaf litter decomposition was equivalent across the edge-to-center gradient in a 10-yr-old landslide. There was significantly higher available soil phosphorus (P) in the landslide center than in the forest for one of two landslides studied by Myster and Fernández (1995).

The abundance of plants, fungi, and birds also change along the edge-to-center gradient. Both vegetation strata and mycorrhizae density increased with proximity to the forest in the Luquillo Mountains on 6- and 20-yr-old landslides; however, this pattern was less pronounced in the plots located in the deposition zone of the landslides

(Myster and Fernández 1995). On two recent landslides in the Luquillo Mountains, seed rain (numbers of seeds m⁻²) tended to increase from landslide interior to edge, and was highest in the forest (Walker and Neris 1993). Additionally, the number of species per seed trap was lowest in the landslide interior relative to the edge and forest (Walker and Neris 1993). Through observations in six landslides in the Luquillo Mountains at different stages of succession, Shiels and Walker (2003) found that birds spent most time at the forest edge relative to the time flying over the landslide or perching on vegetation within the landslide. There are numerous responses to the edge-to-center gradient that occur following landslide disturbance, and many of these responses will influence forest recovery.

The final gradient that is prominent within landslides is the patchiness of the landslide matrix, which largely results from portions of forest that were resilient or otherwise not transported into the deposition zone of the landslide (Fig. 5). Additional patches within landslides can result from variation in underlying substrate (e.g. depth of erosion) and from post-landslide inputs such as sloughing of forest soil into the landslide from the destabilized upper landslide edge. Throughout the temporal gradient of landslide recovery, landslide patches can form and disappear, grow and expand, break apart and shrink, or remain unchanged.

Remnant patches of forest in landslides contain elevated levels of organic matter and nutrients that have been linked to greater size and growth of landslide-colonizing plants in the Luquillo Mountains (Guariguata 1990, Fetcher et al. 1996, Walker et al. 1996a, Shiels et al. 2006). Shiels et al. (2006) experimentally determined the importance of patches of elevated soil organic matter to increases in soil N and seedling growth in landslide soils. In addition to the suite of nutrients contained in organic matter, Zarin and Johnson (1995a) suggested that the presence of soil organic matter in landside soils may be a source of exchange sites where cations that would normally be lost due to leaching are retained. Therefore, the presence of organic matter in landslide soils can increase soil fertility via two simultaneous mechanisms. Using fertilizer additions, Fetcher et al. (1996) determined the importance of N and P patches to growth of pioneer and non-pioneer plant species in young (ca 1.5 yr old) landslide soils. The results of their study showed that both pioneer and non-pioneer plants were N-limited and that pioneer species were additionally limited by P. Using general fertilizers that included macro- and micro-nutrients, Shiels et al. (2006) in the Luquillo Mountains, and Dalling and Tanner (1995) in the Blue Mountains of Jamaica, also determined that nutrients (including N and P) were limiting seedling growth on landslides. In a descriptive study using 30 landslides, Shiels et al. (2008) determined that plant recovery on 14-month-old landslides was controlled by soil factors that included N. Therefore, patches of elevated soil nutrients, particularly N and P, on landslides are commonly associated with

the organic matter reservoirs in forest remnants, and these patches directly enhance plant growth and affect landslide recovery.

In the absence of organic matter, soil nutrient patchiness is prominent in landslides because of the highly variable post-landslide substrate (Guariguata 1990, Zarin and Johnson 1995a, b, Walker et al. 1996a). The depth of soil removed by a landslide is heterogeneous, and can range from areas where only the uppermost topsoil was removed to soil-free patches where only exposed rock remains (Shiels et al. 2008). Weathering of exposed saprolite and bedrock produces patches of soil P, K, calcium (Ca), and magnesium (Mg)-bearing minerals (Zarin and Johnson 1995b). Dips, cracks, mounds, and gullies are additional microhabitat features that contribute to patchiness and can affect the concentrations of readily available nutrients for plant uptake and soil development (Sidle and Ochiai 2006, Shiels et al. 2008). Therefore, soil physical and nutritional characteristics on landslides can vary widely even in the absence of organic matter and forest remnants.

The number and sizes of patches within a landslide can shift through time, further highlighting the dynamic nature of landslides. Post-landslide inputs of nutrients and organic matter may occur by sloughing of forest soil from the forest-landslide edges and from remnant forest patches within the landslide (Adams and Sidle 1987). Inputs of forest soil not only add nutrients and organic matter to landslides, but seeds and microbes such as mycorrhizae commonly accompany the forest soil and possibly facilitate plant recovery (Walker et al. 1996a). Litterfall is an additional input of C and nutrients that is common to landslides of all ages because it can originate from the forest and remnant forest patches in young landslides and from both the forest and landslide colonists in more vegetatively-developed landslides. One caveat that Shiels et al. (2006) uncovered with experimental organic matter additions to landslide soils was that the type of organic matter present in the landslide soil was important for early plant growth and survival, and inputs of forest soil produced positive effects on seedlings but senesced leaves did not. Although leaf litter inputs are often more abundant (potentially creating more patches) than forest soil inputs (Shiels et al. 2008), the short-term (1 yr) effects of leaf litter improving soil nutrients and organic matter are minimal (Shiels et al. 2006), perhaps due to relatively slow decomposition rates in landslides (Shiels 2006). Atmospheric inputs of N, P, Ca, and Mg that are derived primarily from sea salt can range from 0.3 to 15 kg ha^{-1} yr^{-1} in the Luquillo Mountains (McDowell et al. 1990, McDowell and Asbury 1994), which adds yet another source of potential soil nutrient variability within local landslides. Post-landslide erosion can cause microhabitat modifications and shift large amounts (25–80 g d^{-1}) of local surface sediments downslope (Larsen et al. 1998, Shiels et al. 2008, Walker and Shiels 2008). Landslides are dynamic and result in a patchwork of exposed substrates and nutrients following initial disturbance. High levels of sediment wash and inputs from the atmosphere, forest edge, and colonizing biota continue to modify landslide surfaces in the Luquillo Mountains well after the initial disturbance has passed (Shiels et al. 2008, Walker and Shiels 2008).

Conclusions

Storms frequent the Luquillo Mountains in Puerto Rico and trigger numerous landslides along the entire elevation gradient. These landslides are extremely heterogeneous when compared to one another, as well as when viewed individually for the various gradients that they create. The current mosaics of fragmented patches that appear across the mountainscape are often caused by landslides in different locations, clusters, sizes, and successional states. These heterogeneous landslide patches, which represent abrupt gradients in biotic and abiotic conditions, are important for sustaining biodiversity because all stages of successional communities are represented when landslides are viewed on the landscape scale (Elias and Dias 2009, Restrepo et al. 2009). While the elevation gradient in the Luquillo Mountains appears to have minimal influence on landslide abundance and plant development, other gradients such as soil type, slope, age, and distance to edges and the base of a landslide strongly influence plant colonization, growth, and soil development.

Landslides not only create a large number of gradients, but the changes in relative importance of each gradient through succession make landslides dynamic disturbances. Vegetation recovery on landslides can be highly heterogeneous even when landslides are at the same elevation, have the same soil type, and result from the same storm event (Shiels et al. 2008, Walker and Shiels 2008). Such heterogeneity has made it challenging to reach general conclusions about landslides and plant successional processes that go beyond the observation that major life forms occur at different stages of succession and colonize different zones of a landslide (Guariguata 1990, Myster et al. 1997). Such complexity further complicates accurate predictions of the species composition of each successional stage, and if and when a given landslide will resemble a pre-landslide state. The most prominent gradients that are created within landslides include vertical (top to bottom) and horizontal (edge to center) gradients, as well as more abrupt or discontinuous gradients (i.e. patches) largely resulting from forest fragments that were resistant to landsliding (Fig. 5). These gradients clearly affect most, if not all, of the abiotic and biotic factors that comprise landslides and their respective successional trajectories.

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