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Chapter 5 Biotic interactions and temporal patterns forLandslide Ecology

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5 · *Biotic interactions and temporal patterns*

Key points

1. Landslide succession is the sequential replacement of plant commu-
   nities following landslide creation. It is affected by biotic interactions
   and abiotic conditions and occurs in the intervals between recurrent
   erosion events.
2. Plant species can facilitate or inhibit landslide succession by direct
   species interactions or indirectly by the alteration of resources includ-
   ing light levels, soil stability, soil moisture, or soil nutrients. Species
   replacements may also occur due to differences in the life histories of
   landslide colonizers.
3. Herbivores, pathogens, and non-native species influence landslide suc-
   cession and contribute to the variety of successional trajectories found
   on landslides, potentially with long-term consequences.
4. Landslides contribute to temporal heterogeneity of landscapes through
   their destruction and creation of habitats and sharp physical gradients.
   This heterogeneity generally has a net positive effect on biodiversity at
   landscape scales, but landslides generally decrease biodiversity at local
   scales.

5.1 Introduction

As soon as organisms colonize new landslide surfaces, they begin to
alter the environment, often in ways that are not favorable for contin-
ued establishment of additional individuals of the same species. When
changes in the landslide environment favor a new set of species better
adapted to the changing conditions, species replacements occur. This
process is considered succession (i.e., the change of ecological commu-
nities in structure and composition through time) (Glenn-Lewin *et al.*,
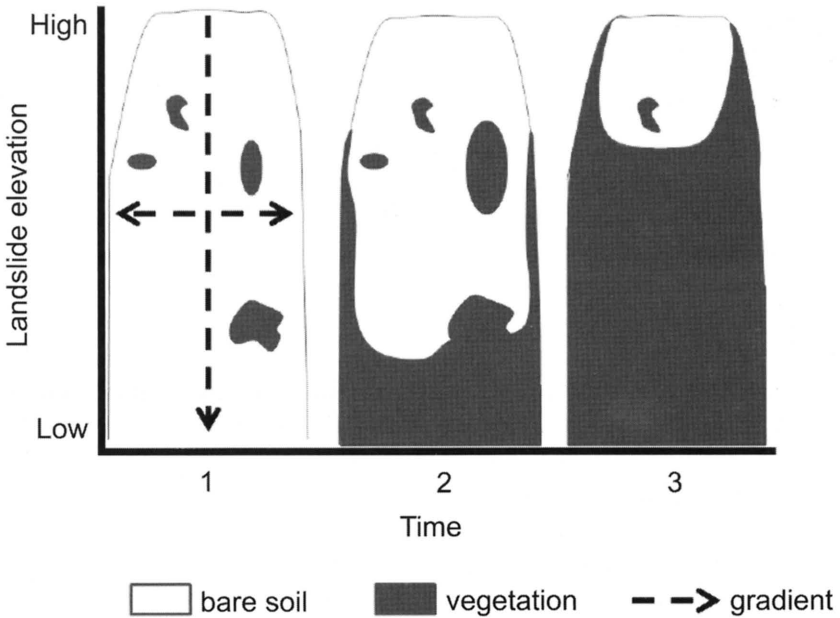1992). Primary succession occurs on surfaces where a disturbance has

Fig. 5.1. Prominent spatial gradients within landslides and their association with patterns of vegetation recovery. Top to bottom and side to side gradients (arrows point toward increasing nutrients and propagule density) are modified by surviving patches of vegetation at time 1. At time 2, vegetation has expanded from the lower edges and enlarging patches. At time 3, all but the slip face and erosion zone just below it have recolonized. From Shiels & Walker (in press) with permission from the Oikos Editorial Board.

left little or no biological legacy (e.g., new volcanic surfaces); secondary succession occurs where soils remain relatively intact (e.g., following logging). Landslides are generally categorized as examples of primary succession because the initial disturbance removes most of the soil and vegetation (Walker & del Moral, 2003). However, because landslides frequently contain remnants of pre-disturbance soils and plants, change on those remnants often occurs along a continuum of disturbance severity between primary and secondary succession (Vitousek & Walker, 1987).

Several cycles of species replacements typically occur during a sere (successional sequence) while the landslide environment is gradually colonized (Fig. 5.1). Within decades, the landslide scar may no longer be visible to the casual observer. Succession can result in the recovery of an ecosystem that resembles the original, pre-landslide ecosystem, but

sometimes new species assemblages are formed. Two or more landslides created at the same time, as well as different locations within the same landslide, may follow similar or different rates and trajectories of succession. These variable pathways enrich the spatial and temporal heterogeneity of landslides and provide a complexity to landslides not always found in other examples of primary succession (Shiels *et al.*, 2008).

Drivers of landslide succession include both regional and local variables where abiotic and biotic factors may drive landslide succession in a hierarchical fashion (Myster *et al.*, 1997). Landslide colonists respond to regional abiotic gradients (e.g., topography, elevation, precipitation) and the regional species pool that determines which species are available and their relative abundance. Landslides contribute to regional biodiversity, particularly when species survive on landslides that cannot survive on less disturbed habitats (see Chapter 4). For example, several species of trees in Patagonia (*Nothofagus* spp., *Fitzroya cupressoides*, *Austrocedrus chilensis*) rely on landslides (and other disturbances including fires and floods) for regeneration (Veblen *et al.*, 1992, 2003) and *Juniperus brevifolia* trees in the Azores rely on landslides, volcanic eruptions, and treefall gaps for regeneration (Elias & Dias, 2004, 2009). The ephemeral nature of many landslides means that they sometimes offer a limited refuge to specialists of disturbed environments.

Local landslide dynamics include abiotic variables such as nutrient availability or surface stability, which affect biotic variables including patterns of species colonization and establishment. Residual soil or surviving organisms can also alter landslide succession. Initially, dispersal and colonization dynamics are important, but as available niches get filled, landslide succession becomes increasingly driven by species interactions; those interactions most carefully examined include facilitation, competition, herbivory, and invasions by non-native organisms. Other potential biotic drivers that are less well studied include mycorrhizae, predation, and disease (Pickett *et al.*, 1987), in addition to the timing of key events in the life cycles of colonizing organisms (e.g., their reproduction, dispersal, and senescence).

Landslides are ecosystems with many spatially and temporally variable habitats which interact with the characteristics of their colonists to shape the still poorly understood process of landslide succession. In this chapter, we summarize what is known about landslide succession, first from a mechanistic perspective of the role of species interactions as drivers of change and then from a landscape perspective of how landslides are a part of larger-scale spatial and temporal dynamics (see Fig. 2.1).

5.2 Succession

5.2.1 Overview

Succession of plant and animal communities has intrigued ecologists for over a century and become the most studied aspect of temporal dynamics, perhaps because of its immediacy and relevance to humans. Many early studies of succession emphasized the role of physical factors. Erosion was recognized as part of a geological cycle of uplift and subsequent erosion (Davis, 1909), but was considered more a background dynamic of all habitats rather than a specific type of disturbance. Cowles (1901) noted that similar results (bare surfaces) such as talus slopes are produced from different processes, including both erosion and deposition. Clements (1928) noted that erosion that creates extensive bare surfaces on slopes and initiates primary succession can be caused by water, wind, gravity, or ice. Clements (1928) also described how low-growing vegetation can help stabilize bare slopes at the surface and how roots can contribute to stabilization at varying depths. Practical efforts such as tree planting began to address slope erosion aggravated by deforestation in the early twentieth century. Efforts in northeastern New Zealand, for example, reduced sediment yield from deforested slopes by 50% within a 10-year period from 1949 to 1958 (Derose et al., 1998). Similar soil conservation efforts were widespread at that time, including in Europe (Coelho, 2006) and North American (Vincent et al., 2009).

Vegetation dynamics on landslides (sometimes explicitly addressing successional changes) were not examined extensively until the mid to late twentieth century, mostly in studies from temperate climates found in North America (Langenheim, 1956; Flaccus, 1959; Miles & Swanson, 1986; Adams & Sidle, 1987), South America (Veblen & Ashton, 1978; Veblen et al., 1980), New Zealand (Mark et al., 1964; Johnson, 1976), Australia (Melick & Ashton, 1991), Africa (Lundgren, 1978), and Asia (Pandey & Singh, 1985). Studies of vegetation dynamics on tropical landslides followed, particularly in the Caribbean (e.g., Garwood, 1985; Guariguata, 1990), and within a decade numerous aspects of landslide succession could be summarized (Walker et al., 1996). Landslides have also been studied as parts of regional disturbance regimes. Garwood et al. (1979) found that landslides covered up to 10% of certain regions in Panama and 49% in New Guinea, while Restrepo & Alvarez (2006) determine that at least 0.3% of Central American montane ecosystems were affected by landslides each century. Matthews (1992) recognized landslides as a disturbance associated with glacial moraines and Oliver

Drivers

Regional conditions — Geology Climate

Local conditions — Topography Soil Species pools Disturbance regimes

Disturbance — Landslide

Microsite conditions — Legacies Nutrients Carbon

Successional responses — Colonization Emigration Replacement Maturation Senescence — Re-sliding

Mechanisms — Life histories Competition Facilitation
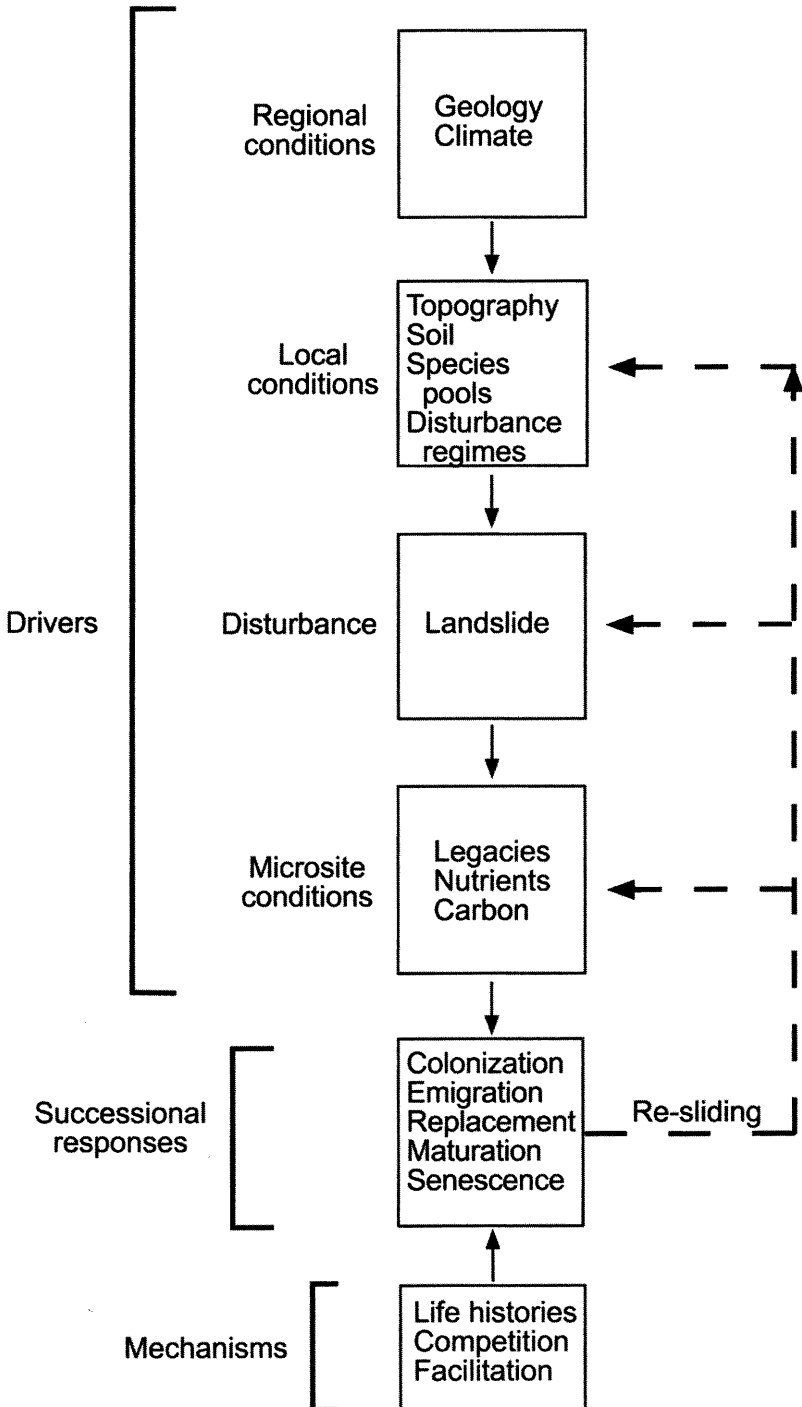
et al. (1985) estimated that nearly 25% of a deglaciated area in Washington, U.S. was subject to rock slides. Landslides can also be triggered by dunes, earthquakes, floods, mines, roads, and volcanoes. Succession has been monitored closely on the resulting surfaces (Crisafulli *et al.*, 2005; Dale *et al.*, 2005). Landslides can, in turn, trigger floods, treefalls, and herbivore outbreaks, among other disturbances (Walker, 1999). For example, landslides frequently dam rivers and cause flooding when the dams erode (see Chapter 2; Schuster, 1995). Interest in landslide succession has developed in part from concerns about landslides as hazards to human lives and properties (Cruden & Fell, 1997; Petley, 2010) and in part from the need to conserve (Usher & Jefferson, 1991; Usher, 1993) and restore (Pandey & Singh, 1985; Chaudhry *et al.*, 1996) their unique ecosystems (see Chapter 6). As noted in Chapter 1, geological studies of landslides have a longer history than ecological studies and provide an excellent source of information on temporal changes in the physical aspects of landslides (Sharpe, 1960) and practical tools for predicting and mitigating landslide hazards (see Chapter 6).

Factors that affect landslide succession are complex, incorporating both abiotic and biotic features of an ecosystem. Geology and climate provide the regional conditions, which over time determine the local conditions of topography, soils, species pools, and disturbance regime (Fig. 5.2). The abiotic features of the disturbance (intensity and severity) determine the

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Fig. 5.2. Major drivers of landslide succession. Drivers of landslide succession are presented as a hierarchy of long and large regional drivers (geology and climate) that direct local conditions of topography (slope, aspect), soil status (chemistry, texture, stability, and organic content), and the pool of available species (regional fauna and surrounding vegetation and its phenological status). The current disturbance regime is also influential in determining the course of landslide succession. Once a landslide is triggered, microsite conditions drive the successional response. These conditions include legacies of undisturbed patches of soils or seed banks, nutrient inputs (mineral weathering, atmospheric deposition, bird inputs, nitrogen fixation, plant uptake) and outputs (leaching, denitrification, volatilization), and carbon inputs (plant litter, dead animals, rafts of surrounding soils) and outputs (erosion). Microsite conditions constrain the process of landslide succession through their influence on colonization (wind, water, and animal dispersal), emigration (of colonists as high-light niches fill), species replacements (driven by the mechanisms of competitive, facilitative, and neutral, life history–related interactions), maturation (increases in nutrients, biomass, mycorrhizae, seed banks but decreases in light and erosion rates), and senescence of canopy vegetation (more light and erosion but less biomass and available nutrients). Re-sliding (dotted lines) effectively resets landslide succession through its influences on microsite and local conditions.

conditions upon which the successional response proceeds. Many other variables provide site conditions that influence successional responses, particularly the changing availability of resources such as nutrients and carbon that can move in or out of a landslide during succession. Walker *et al.* (1996) proposed that soil stability and fertility determined successional pathways on Puerto Rican landslides (Fig. 5.3). Further evaluation of this model suggests that soil nitrogen and slope stability are both important (Shiels *et al.*, 2008) and that organic carbon is more likely to come from sloughing of forest soil into the landslide than from growth by new colonizing plants (Shiels *et al.*, 2006). In general, a young landslide is characterized by high light, low soil nutrients, and low biomass; an older landslide is usually more shaded and more nutrient- and biomass-rich (see Chapters 3 and 4).

The biotic response to site conditions is the sequential replacement of plant and animal communities, which is a function of their life history characteristics and interactions (positive, negative, or neutral). Interactions that promote successional change are considered facilitation while interactions that delay successional change are considered competitive inhibition (Table 5.1). These processes are not exclusive, can be "turned on" or "turned off" (Odum 1959; Walker, 2012), and can even co-occur or vary in sequence, so it is the relative balance of all species interactions that drives successional change (Walker & Chapin, 1987; Callaway & Walker, 1997). Herbivory (see Section 5.2.5) and non-native species (see Section 5.2.6) can also affect successional dynamics on landslides, sometimes in unexpected ways. Successional trajectories are therefore determined by the mutual influences of abiotic factors such as post-landslide erosion, cyclones, soil texture and moisture, and microclimates (Fig. 5.4; see Section 3.3.2) and biotic factors such as species composition and relative abundances, above-ground structure and growth rates, and root densities. When erosion re-occurs, landslide succession is reset, but it can take either a similar or a different trajectory (see Section 5.2.7). The numerous variables that influence landslide succession make predictability low, although similar responses to limiting variables can occur among groups of landslides (Shiels *et al.*, 2006).

The importance of facilitative interactions is likely to be higher in early than late succession because of the difficulties of establishing in a harsh environment (see Section 4.3; Walker, 1999). Competitive interactions often dominate later, as competition among plant species for nutrients, water, and light becomes more intense (Walker & Chapin, 1987). Landslides are a good place to examine interactions among species because
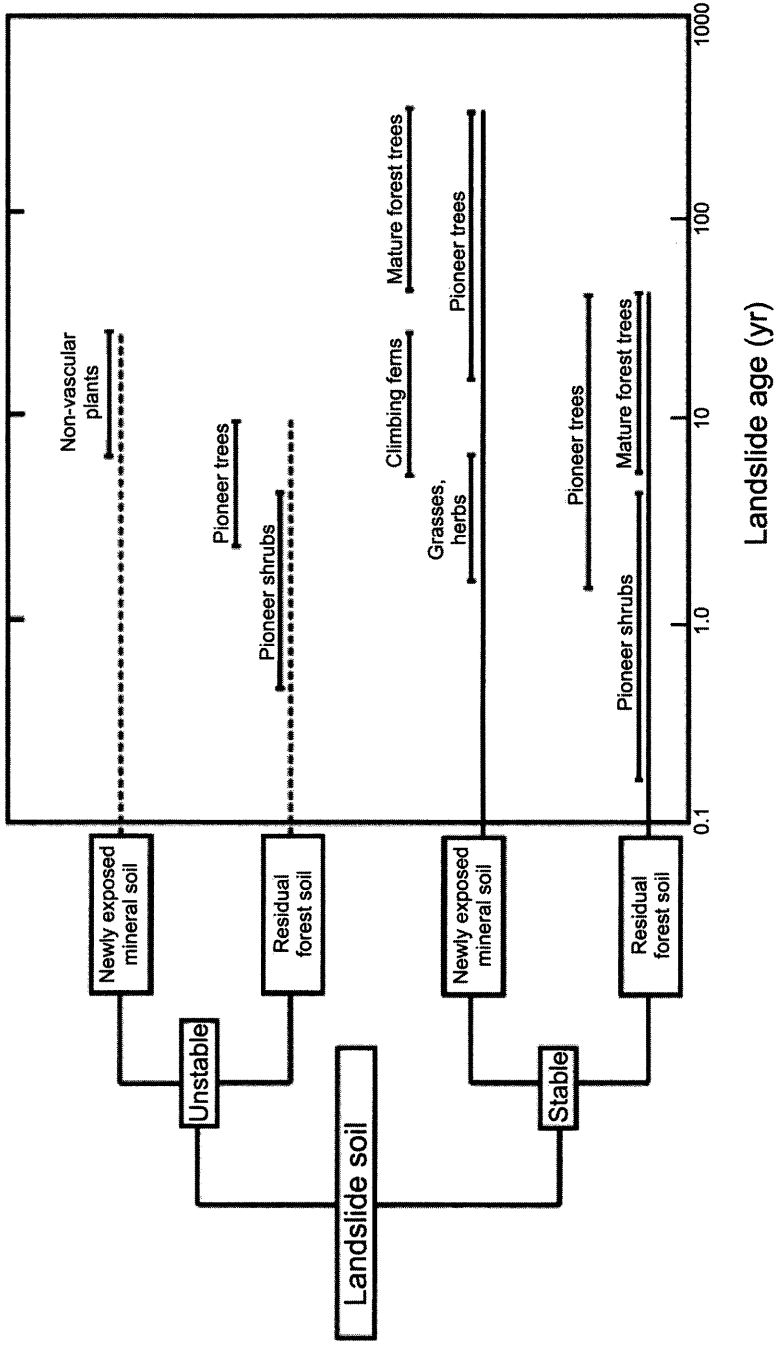
Fig. 5.3. Four proposed successional trajectories for Puerto Rican landslides, depending on soil stability and organic content (highest in residual forest soils). Succession proceeds most rapidly on stable, organic soils. From Walker *et al.* (1996), with permission from John Wiley & Sons.

Table 5.1. *Types of species interactions in primary succession on landslides*

Interaction type	Description	Successional implications and mechanisms	Selected references (see text for more)
One-way			
+	Obligatory facilitation	Succession only if facilitator present	Clarkson & Clarkson, 1995
+	Facultative facilitation	Accelerates succession	
	Direct	Dispersal	Shiels & Walker, 2003
	Indirect	Site amelioration	
	Immediate		Dalling & Tanner, 1994; Walker, 1994
	Delayed		Chaudhry et al., 1996; Shiels et al., 2008
−	Competitive inhibition	Delays succession	
	Direct	Removes light, water, nutrients; prevents germination	Veblen et al., 1980; Reddy & Singh, 1993; Velázquez & Gómez-Sal, 2009a,b
	Indirect	Changes disturbance regime	Singh et al., 1984; Velázquez & Gómez-Sal, 2007
+/−	Commensalism	Nurse plants	Guariguata, 1990; Francescato et al., 2001
Two-way			
0/0	Tolerance	No direct interactions among species	Pandey & Singh, 1985
+/+	Double facilitation	Mutualisms, nurse plants that benefit	Chaudhry et al., 1996
+/−	Contramensalism	Facilitator later out-competed	Francescato et al., 2001
−/+		Inhibition benefits inhibitor	Claessens et al., 2006[1]
−/−	Competitive inhibition (or competitive displacement)		
	Non-hierarchical	Effects depend on life histories	Walker et al., 2010a
	Hierarchical	Increasing competitiveness during succession	Pandey & Singh, 1985; Velázquez & Gómez, 2009a[2]
Three-way	Indirect facilitation or competition	Promotes species diversity	Walker et al., 2010a
	Differential response	Promotes species diversity	Bellingham et al., 2001
	Cyclical	Promotes species diversity	Kessler, 1999; Elias & Dias, 2009

[1] Competitively superior on new landslide scars.
[2] Asymmetric, intraspecific competition for light.
+ = facilitation, − = competitive inhibition, 0 = no interaction. Modified from Walker & del Moral (2003).

(a)

Fig. 5.4. Successional sequence on landslide ES-1 near the El Verde Field Station, Luquillo Mountains, Puerto Rico. (a) 6 mo; (b) 18 mo; (c) 22 mo (note Hurricane Hugo damage to young *Cecropia schreberiana* stems seen in (b); and (d) 80 mo (note full canopy of *Cyathea arborea* tree ferns). Photographs by L.R. Walker.

(b)

Fig. 5.4. (cont.)

(c)

Fig. 5.4. (cont.)

(d)

Fig. 5.4. (cont.)

they provide sharp physical gradients where the relative importance of different types of interactions can be contrasted (Shiels & Walker, in press; Walker, 2011).

5.2.2 Facilitation

The harsh physical environment typical of early primary succession can be quite difficult for potential colonists to tolerate. New landslide surfaces can be exposed to winds and rains and vulnerable to secondary erosion; a lack of shade can result in extreme temperature ranges and soil nutrient levels are generally low (see Section 3.4.2). For some species, however, landslides provide a favorable habitat to establish, particularly if the species are not adapted to the shade and root competition of adjacent forest understories (Dalling & Tanner, 1995) or because they are small-seeded (Metcalfe *et al.*, 1998) and require exposed soil surfaces free of obstructing leaf litter (e.g., *Clethra occidentalis* in Jamaica). A plant species that establishes a resident population in such environments can ameliorate the harshness for other species, thereby facilitating their dispersal, colonization, growth, reproduction, or survival (Bellingham *et al.*, 2001; Walker & del Moral, 2003). For example, on landslides in southern New Zealand, *Leptospermum scoparium* is a shrub that apparently facilitates succession by ameliorating new landslide scars and promoting establishment of later successional trees (Mark *et al.*, 1989). Facilitation can be direct when another species is the direct benefactor of the facilitator (e.g., when the facilitator protects another species from herbivory). Facilitation can be indirect through general (not species-specific) habitat amelioration (e.g., improved soil fertility), or when species that inhibit successional turnover are themselves inhibited (a three-way interaction). Facilitation can alter the rate of turnover among successional stages, frequently by accelerating community change. In some successional models, facilitation was thought to be obligatory, whereby the environmental changes that the first colonists made were required for the second wave of colonists (obligatory facilitation or relay floristics model; Clements, 1916; Egler, 1954; Connell & Slatyer, 1977). A corollary to this facilitative effect was the idea that the changes made by the first colonists did not improve their own chances of reproduction so they were eventually replaced. However, there is much more evidence for facultative succession (optionally facilitative) than obligatory succession (where facilitation is required; Walker & del Moral, 2003). Facilitation is now recognized as just one of many contributing factors driving landslide succession.

Evidence for facilitation of landslide succession comes from several sources and includes direct facilitation, indirect facilitation through habitat amelioration, or indirect facilitation through three-way interactions. Direct facilitation occurred on Puerto Rican landslides when trees facilitated bird dispersal of seeds of forest species (see Fig. 4.2; Shiels & Walker, 2003). Indirect facilitation occurred on several tropical landslides where fast-growing pioneer trees such as *Trema micrantha* (Vázquez-Yanes, 1998; Velázquez & Gómez-Sal, 2009a) and *Cecropia schreberiana* (Brokaw, 1998) produced shade and abundant leaf litter that moderated temperature and moisture extremes and improved soil stability and nutrient availability. Similarly, *Alnus nepalensis* was effective in ameliorating landslide soils in the Himalayan Mountains of India because its nitrogen fixing abilities, fast growth, and copious leaf litter improved soil nutrients and organic matter (Chaudhry *et al.*, 1996). Miles *et al.* (1984) also noted the importance of *Alnus rubra* on landslides in Oregon where it was a dominant pioneer. The facilitative role of nitrogen fixing plants is well recognized in primary succession, including on landslides (Walker & del Moral, 2003). In one survey, nitrogen fixing plants were of intermediate abundance on landslides (mostly as herbaceous legumes or actinorhizal plants) compared to glacial moraines where they were more abundant, and volcanic surfaces where they were less abundant (Walker, 1993). The facilitative role of nitrogen fixers can be overstated because the nitrogen fixing plant may dominate available resources and recycle its own nutrients, which in turn delays succession (Walker, 1999; Pabst & Spies, 2001; Halvorson *et al.*, 2005). Alternatively, both the nitrogen fixer and adjacent plants can benefit, in a two-way mutualism or double facilitation (Chaudhry *et al.*, 1996). Another mode of facilitation from habitat amelioration comes from dense thickets of Gleicheniaceae ferns that stabilize landslide soils (Fig. 5.5(a); Shiels *et al.*, 2008), permit the buildup of soil organic matter, soil nitrogen, and soil moisture (Walker, 1994; Walker & Shiels, 2008), and provide shade that can promote germination of woody colonizers (Ohl & Bussmann, 2004), such as *Tabebuia heterophylla* on Puerto Rican landslides (Walker, 1994). Finally, three-way facilitation occurred when Puerto Rican landslides were colonized by woody pioneers that indirectly facilitated succession to late successional forests by inhibiting the growth of vines, forbs, grasses, and thicket-forming ferns (Gleicheniaceae); these herbaceous plants, in turn, inhibited late successional tree growth, so the inhibition of an inhibitory interaction results in net facilitation (Walker *et al.*, 2010a). Another type of three-way interaction occurred on New Zealand landslides where several tree

(a)

Fig. 5.5. Thickets of colonizing plants on Puerto Rican landslides.
(a) Gleicheniaceae ferns (*Sticherus bifidus* & *Gleichenella pectinata*); (b) forbs and
graminoids; and (c) tree ferns (*Cyathea arborea*). Photographs by A.B. Shiels
(a) and L.R. Walker (b), (c).

species responded differently to facilitation by a nitrogen fixing shrub
(Bellingham *et al.*, 2001).

5.2.3 Competition

Interspecific competition, or the negative effect of one species on
another, has an important role in directing successional trajectories. Cer-
tain species slow or arrest succession by preventing establishment of
species representing the next successional stage, either by resource pre-
emption or antagonistic effects (allelopathy). This process is called com-
petitive inhibition and can last as long as the inhibitor lives. Competitive
displacement, on the other hand, involves one species replacing an estab-
lished species (Walker & Chapin, 1987) and can accelerate succession.
Competition for resources often focuses on light (particularly in mid to
late stages of succession) and nutrients (often in early and late stages).

(b)

Fig. 5.5. (cont.)

Late successional declines in productivity and nutrient availability (and concomitant increases in light) can result from long-term resource consumption and leaching. These declines are termed retrogression and may occur over millions of years (Peltzer *et al.*, 2010). Species replacements

(c)

Fig. 5.5. (cont.)

may, in some cases, be largely determined by the initially decreasing and eventually increasing light:nutrient ratios (Tilman, 1985) as suggested for succession to oak forests on several Himalayan landslides (Reddy & Singh, 1993).

Thicket-forming species are often inhibitors of succession on landslides (Langenheim, 1956; Velázquez, 2007) for several reasons. They typically take advantage of the high light, low nutrient conditions; spread vegetatively; and, through their dominance of early successional resources, reduce or eliminate establishment of later successional plants. The inhibitory effects of thicket-forming species are related to their longevity, size, canopy cover, and density relative to similar characteristics of species of later successional plants (Walker *et al.*, 1996; Callaway, 2007). Thicket-formers on landslides can be trees (Reddy & Singh, 1993; Pabst & Spies, 2001), shrubs (Langenheim, 1956), ferns (Guariguata, 1990; Walker, 1994; Walker *et al.*, 2010a), or forbs and graminoids (Fig. 5.5; Velázquez & Gómez-Sal, 2009b; Walker *et al.*, 2010a). For example, where pine trees (*Pinus roxburghii*) were the initial colonizers of landslides in the central Himalayas, they maintained their dominance throughout

a 25 year chronosequence (Reddy & Singh, 1993). The low nutrient content of pine litter likely inhibited the invasion of oak trees (*Quercus leucotrichophora*; Singh *et al.*, 1984). Similarly, the dense shade of *Alnus rubra*, the dominant tree in early succession on landslides in coastal Oregon (U.S.), led to the decline or elimination of forbs and tree seedlings of other species, even those of the shade-tolerant *Tsuga heterophylla* (Pabst & Spies, 2001).

Scrambling ferns in the Gleicheniaceae are the first colonizers on many tropical landslides (see Section 4.5.2) and typically form thickets that can delay forest succession for several decades by monopolizing resources (Walker & Sharpe, 2010). Their dispersal by spores, subsequent vegetative expansion with indeterminate growth, dense layers of senesced leaves and rhizomes up to several meters thick, live rhizome mats, slow decomposition, rapid recovery after fire, and potential allelopathic traits make them effective inhibitors of landslide succession (Fig. 5.6; Slocum *et al.*, 2004, 2006; Walker *et al.*, 2010a). While there can be some promotion of germination of tree seeds under scrambling fern thickets, perhaps due to higher soil water, early seedling growth is inhibited by the 12- to 100-fold reduction of light levels under the thickets (Walker, 1994; Shiels & Walker, 2003). Dead rachises and leaflets remain for several years on the live portion of the leaves, contributing to the reduction of light transmission to the landslide surface. Rhizome mats can also develop that are > 30 cm deep (Slocum *et al.*, 2004), further deterring the establishment of other plants. For example, more seeds of forest species were found on landslides in Puerto Rico that were bare or covered with grass than on landslides covered with scrambling fern thickets (Shiels & Walker, 2003). Even if seeds of forest species were able to germinate, their lack of contact with mineral soil would limit growth. In addition, the slow decomposition of scrambling ferns immobilizes nitrogen and phosphorus (Maheswaran & Gunatilleke, 1988), but may allow the gradual accumulation of soil carbon (Russell *et al.*, 1998; Walker & Shiels, 2008) and long-term erosion control on landslides.

Tree fern thickets can also inhibit landslide succession (Fig. 5.5(c); Walker *et al.*, 2010a). Tree ferns are common landslide colonists (see Section 4.5.2; Walker & Sharpe, 2010) and tend to outcompete scrambling ferns in fertile patches on landslides in the Dominican Republic (Slocum *et al.*, 2006), Tanzania (Lundgren, 1978), Bolivia (Kessler, 1999), and New Zealand (Stewart, 1986). In addition to reducing light levels, they tend to sequester a high proportion of available nutrients (Vitousek *et al.*, 1995). On several Puerto Rican landslides, decomposition rates

Fig. 5.6. Dense mats of dead rachises and live rhizomes of two ferns in the Gleicheniaceae (*Sticherus bifidus* and *Gleichenella pectinata*). Photograph by L.R. Walker.

of the dominant tree fern (*Cyathea arborea*) were higher than those of the dominant woody species (*Cecropia schreberiana*; Shiels, 2006), suggesting that dominance in that case was due to characteristics other than nutrient immobilization. Tree ferns can facilitate the growth of epiphyte

communities on their trunks or serve as nurse logs for both herbaceous and woody plant species (Walker & Sharpe, 2010).

Many thicket-formers are weedy plants promoted by human activities such as fire (Velázquez & Gómez-Sal, 2009b). For example, in areas adjacent to a large landslide in Nicaragua, farmers commonly burned crop residues during the dry season. These fires expanded into the landslide where the fire-prone grass *Hyparrhenia rufa* was dominant, creating a positive feedback loop because the grass returns quickly after being burned (Velázquez & Gómez-Sal, 2007). In contrast, in Taiwan, the aggressive native grass *Arundo formosana* helped stabilize landslides, reducing erosion by 80% in 6 years without human intervention (Lin *et al.*, 2006). Alternatively, grass cover can be replaced within several years by vegetative expansion of nearby scrambling ferns, particularly when soil nutrients remain at levels that limit the establishment of forest species (Walker & Boneta, 1995). Scrambling ferns may (Aragon, 1975) or may not (Walker, 1994) be allelopathic, but their other traits make them effective inhibitors in landslide succession (Slocum *et al.*, 2004). Ultimately, despite their initial inhibitory effects, scrambling ferns may have a delayed and indirect facilitative effect on landslides, where they increase soil stability and increase soil organic matter, thereby improving the conditions for later successional species (Shiels *et al.*, 2008; Walker & Shiels, 2008). Thicket-forming species, therefore, can have both negative and positive influences on landslide succession (Fig. 5.7).

Intraspecific competition for resources occurs among the same species. This type of interaction can have successional implications on the wide range of habitats that landslides present, particularly when the species of concern is dominant across that range. On a large Nicaraguan landslide, Velázquez & Gómez-Sal (2009a) found evidence supporting intraspecific competition among populations of *Trema micrantha*, a common woody pioneer of disturbed tropical environments (Garwood, 1985; Campanello *et al.*, 2007). In fertile and stable depositional zones, *T. micrantha* individuals competed with each other through asymmetric competition for limiting light (the tallest trees won). The short-stemmed individuals that survived during the 2 year study period were ones that grew rapidly in height. In less stable erosional zones of the landslide, which were also relatively low in soil nutrient availability, *T. micrantha* individuals did not develop canopy hierarchies. Instead, all individuals remained small, although those with greate diameter growth were more likely to survive. *Trema micrantha* is clearly a versatile type of pioneer species that is able to allocate resources to height or diameter
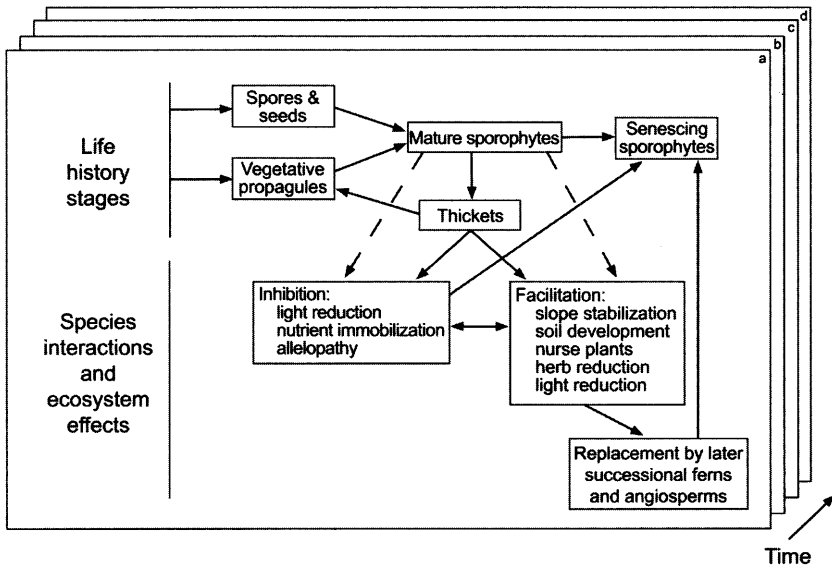
Fig. 5.7. Thicket effects on landslide succession. Dispersal of spores and seeds or vegetative propagules to a site results in development of mature sporophytes that eventually senesce. Sporophytes can either inhibit or facilitate transitions to sequential successional stages (planes b, c, d, etc.) as individuals (dotted arrows) or through a variety of changes that thickets create in the local environment. Modified from Walker & Sharpe (2010) with permission from Cambridge University Press.

growth depending on the landslide environment that it inhabits. Such versatility suggests that its use as a stabilizer of disturbed habitats for restoration activities is warranted (Velázquez & Gómez-Sal, 2009a). Intraspecific competition is likely a common feature among thicket-forming species on landslides.

5.2.4 Life history characteristics

When species growing together do not appear to facilitate or compete with each other, the tolerance model of succession can be applied (Connell & Slatyer, 1977). This model is sometimes associated with the initial floristics model (Egler, 1954), which suggests that many species arrive early in succession but that sequential dominance occurs due to variability in lifespans and serial conspicuousness (visual dominance). However, in Connell & Slatyer's original model, although species initially do not interact immediately following a disturbance, later success is achieved

by the species that can best tolerate reduced resource levels. This process is essentially a form of competitive displacement (Walker & Chapin, 1987). On some Himalayan landslides, pioneer annual forbs persisted throughout 40 years of succession, even while perennials gradually gained dominance (Pandey & Singh, 1985). Thus, there was a gradual shift of dominance without any clearly defined successional stages. On landslides in northern New Zealand, kauri trees (*Agathis australis*) are early colonists that are also long-lived. This combination of traits plus return intervals of landslides that are frequently within the lifespan of a given tree allow the kauri trees to out-compete angiosperm tree species (Claessens *et al.*, 2006) in a type of relationship where the inhibition benefits the inhibitor (contramensalism) (Table 5.1). Similarly, *Fraxinus platypoda* trees are frequent and abundant colonists of landslides in Japan, forming dominant, single-cohort forests (Sakio, 1997).

Life forms are often a factor in determining the nature of an interaction between two species. For example, on Bolivian landslides scrambling ferns and club mosses were early colonists and may facilitate succession by stabilizing the surface (Kessler, 1999). They were outcompeted by tree ferns, which were, in turn, outcompeted by forest tree species. Some tree ferns remained but eventually died from senescence, and forest canopies tended to open up with age from intraspecific competition (self-thinning, *sensu* Westoby, 1984) and senescence. A second period of inhibition of tree establishment by scrambling ferns then occurred, as the ferns more readily colonized forest gaps than did tree seedlings. Intriguingly, fern species richness did not necessarily decline, but rather shifted to yet another life form – the emergence of epiphytic ferns on remaining tree ferns and tree trunks (Kessler, 1999). Thus, even within a single taxonomic group such as ferns, life forms have a role in determining patterns of landslide succession. Similar shifts in fern life forms occurred on Hawaiian landslides (Restrepo & Vitousek, 2001), with the erect but short *Nephrolepis multiflora* and the creeping but open-canopied *Odontosoria chinensis* dominating for the first several decades, followed by the denser canopies of the scrambling ferns and tree ferns. Tree ferns were present in mature forests in Hawaii (Restrepo & Vitousek, 2001), unlike Caribbean forests where tree ferns are largely restricted to landslides and other gaps (Slocum *et al.*, 2006; Walker & Sharpe, 2010). On Japanese landslides, herbaceous life forms colonized first, followed by shrubs and then trees; one of these colonists (a grass, *Miscanthus sinensis*) may facilitate the establishment of woody species by stabilizing landslide soils (Nakamura, 1984). Similarly, large moss cover on Ecuadorian landslides

enhanced germination of woody pioneers both by compensating for the loss of water after a landslide and by facilitating scarification of seed coats (Myster & Sarmiento, 1998). Mosses also facilitated woody species establishment on landslides in the Azores on the most stable sites. However, on unstable portions of the landslides, the moss carpets, which can reach 1 m in depth, increased the risk of re-sliding when they absorbed large amounts of water (Elias & Dias, 2009). The influence of life form on landslide dynamics is therefore not always predictable.

Life stage is another determinant of the balance between facilitative and competitive interactions (Walker & del Moral, 2003; Walker *et al.*, 2003) in landslide succession, as seen from some of the examples already discussed. Each stage in the life of an organism, including dispersal, germination, establishment, growth, survival, and reproduction, can potentially be facilitated or inhibited by other species (Walker, 1994; Shiels & Walker, 2003; Walker & del Moral, 2003; Slocum *et al.*, 2004; Cammeraat *et al.*, 2005; Velázquez, 2007). Dispersal can be facilitated by trees that provide birds a place to perch and defecate seeds onto landslides, but those trees or other ground cover that attracted the birds can also inhibit establishment through their shading and leaf litter (Shiels & Walker, 2003). Woody plant germination can be facilitated by ferns from the Gleicheniaceae on Puerto Rican landslides, but when trees overtop the ferns, they can eventually outcompete and replace them (Walker, 1994). Establishment, growth, and survival are facilitated by species that stabilize the slope, ameliorate the microsite, or decrease the frequency or intensity of other types of disturbances such as secondary erosion. For example, on abandoned agricultural terraces dominated by fruit trees in a landslide-prone area of Spain, grasses and forbs were the initial colonists and they contributed to the development of soil strata, aeration, and carbon accumulation as well as to a reduction in surface erosion (flow; Fig. 5.8; Cammeraat *et al.*, 2005). These changes likely facilitated the establishment and growth of later successional shrubs (*Ulex parviflorus* and *Crataegus monogyna*) and trees (*Pinus halepensis*). Finally, reproduction can be facilitated by species that provide food for pollinators, or otherwise promote reproduction (Walker & del Moral, 2003), although we know of no evidence for this hypothetical interaction on landslides.

5.2.5 Herbivory and pathogens

Herbivory has been recognized as an important plant–animal interaction in secondary (Brown & Gange, 1992) and primary (Walker & del
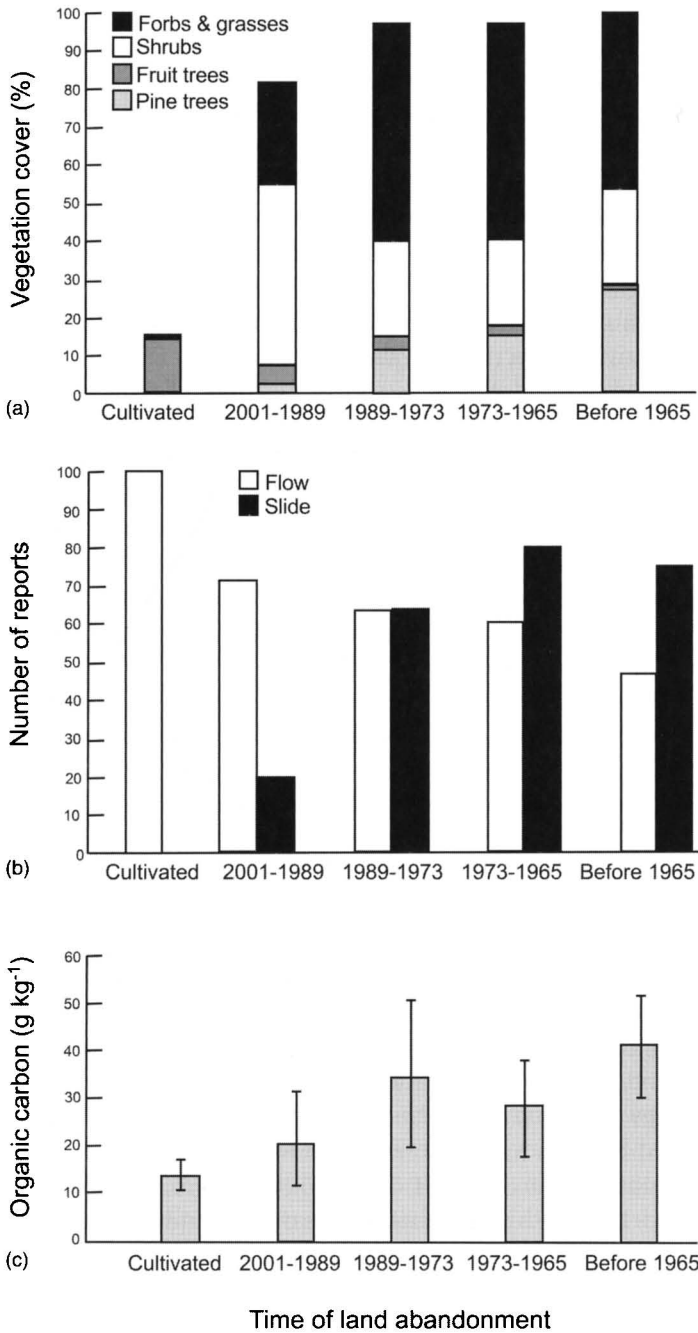
Fig. 5.8. Changes in (a) vegetation cover, (b) erosion type, and (c) soil organic carbon (mean ± S.D.) following abandonment of agricultural terraces in Spain. From Cammeraat *et al.* (2005) with permission from Springer.

Moral, 2003) succession. Granivores can influence colonization of landslides. Black rats (*Rattus rattus*) are a formidable seed predator in most ecosystems where they have been introduced (Towns *et al.*, 2006; Shiels & Drake, 2011), and droppings of these rats were found on Puerto Rican landslides (Shiels, 2002). Seed predation by insects has been reported for *Cecropia schreberiana* in Puerto Rico and for *Urera caracasana* and *Witheringia coccoloboides* in Costa Rica, but fungal pathogens may have caused more seed loss than predation (Myster, 1997).

Herbivory can slow successional change when a plant facilitator is negatively affected by herbivory. For example, stem borers and leaf miners periodically damage thick stands of the nitrogen fixing herb *Lupinus lepidus* that have colonized the erosive volcanic slopes of Mount St. Helens since its 1980 eruption (Fagan & Bishop, 2000). Herbivory can accelerate succession when early successional species are preferred. For example, seedlings of *Salix* spp. and *Populus balsamifera* trees are preferred by hares (*Lepus arcticus*) and moose (*Alces alces*) over seedlings of *Picea glauca* trees on central Alaskan floodplains (Bryant & Chapin, 1986). Sometimes disturbances can temporarily reduce herbivore pressure in succession. In the Aleutian Islands of Alaska, for example, *Lupinus nootkatensis* is one of just a few species to establish successfully (from surviving, buried propagules) on the newly ash–covered and highly erosive slopes of Kasatochi Volcano (Fig. 5.9; Box 5.1; Talbot *et al.*, 2010). However, the 2008 eruption apparently destroyed populations of its most abundant insect herbivores (Sikes & Slowik, 2010), giving *L. nootkatensis* a temporary reprieve from herbivory (except by some hungry gulls; Plate 14). *Lupinus nootkatensis* appeared most robust in the deposition zone of landslides below cliff bases where erosion of new ash deposition has been rapid (Talbot *et al.*, 2010). Herbivory is often stage-specific, especially when its host population is not an early colonizer. For example, the largely coniferous forests in the Rocky Mountains of Colorado (U.S.) do not sustain large insect outbreaks until trees reach at least 70 years of age. In regions where snow avalanches regularly kill the dominant *Picea engelmannii* trees, insect herbivores have a minor role in the early decades of plant succession (Veblen *et al.*, 1994). Alternatively, early successional vegetation and distinct microclimates found on landslide scars can attract both insect and mammalian herbivores. Effects of herbivory on plant succession can be difficult to distinguish from other factors governing changes in species composition. In the landslide-strewn Kokatahi Valley in New Zealand, non-native possums (*Trichosurus vulpecula*) have been suggested as causes of the decline in late successional, native forests dominated by

Fig. 5.9. An earth flow on the rapidly eroding ash deposits from a 2008 eruption of Kasatochi Volcano, Alaska. See Box 5.1. Photograph by L.R. Walker.

Metrosideros umbellata and *Nothofagus* spp. (Rose *et al.*, 1992). However, cohort senescence of the trees, inhibition of germination by litter of other species, increased landslide or earthquake frequency, or climatic shifts may also influence succession (Veblen & Stewart, 1982; Allen *et al.*,

Box 5.1 Plant succession despite high rates of erosion

When Kasatochi Volcano erupted in 2008, it provided an excellent laboratory to study primary succession. Lawrence and other scientists have been visiting the island each year since it erupted to document the rapid changes. The eruption deposited tens of meters of ash on Kasatochi Island in the Aleutian Islands, Alaska. Rapid erosion of that ash in debris slides and debris flows has led to the formation of one 40 m deep canyon and many smaller gullies and rills across the southern slopes of the island (Fig. 5.9). Following the eruption, volcanic ash eroded at rates of 10^4 m^3 km^{-2} $year^{-1}$, causing the shoreline of this 3 km diameter island to recede about 100 m (Waythomas et al., 2010). Colonists of this largely barren, landslide-covered landscape appear to be almost entirely from survivors of the eruption. Plants that survived as roots, underground stems, or seeds, including *Lupinus nootkatensis* (Plate 14), are now slowly expanding in areas where the ash layer was eroded (e.g., cliffs and cliff bases, landslides, and bluffs) (Talbot et al., 2010). About 500 000 seabirds, half of which were least auklets (*Aethia pusilla*), nested on the island prior to the eruption and are now attempting to nest again. However, the rock crevices and vegetation that they and other seabirds prefer for nest sites are still unavailable. Once seabird colonies re-establish, they will have a strong positive effect on soil nutrients and therefore on plant succession. Gulls are introducing some dead plant matter from other islands (the nearest are 25 km away) to make their temporary nests, but no germination has been observed at these scattered gull nests. Gull colonies have altered primary plant succession on other volcanoes in Iceland (Magnússon et al., 2009), New Zealand (Clarkson & Clarkson, 1995), and elsewhere (Walker, 2012) by introducing plants and fertilizing the nutrient-poor volcanic substrates. For now, we have the unusual situation that plant growth is limited to survivors of the eruption with no significant inputs from elsewhere. Areas of active erosion are removing many of the few survivors (Plate 8), but are also uncovering others, so expansion of the vegetation is beginning.

2003), confounding any simple interpretation of the role of herbivory (Bellingham & Lee, 2006).

Biotic interactions such as herbivory and plant pathogens are potentially weaker on tropical islands than on continents due to shorter

periods of co-evolution (Janzen, 1973; Augspurger, 1984). In contrast, island flora and fauna are highly vulnerable to recently introduced herbivores and pathogens for which they have not evolved any defenses (Atkinson, 1989; Courchamp & Caut, 2005). Weaker interactions might have less influence on succession than strong ones. However, Myster (1997) did not find differences in levels of herbivory between Puerto Rican and Costa Rican landslides. Myster (2002) also examined insect herbivory and foliar pathogens on two landslides in Puerto Rico and found < 7% leaf loss in *Cecropia schreberiana*, a common woody landslide colonist, and 25%–34% leaf loss for *Inga vera*, a nitrogen fixing tree, which is a later colonizer of landslides and forest gaps. Continental studies had generally equivalent or lower levels of herbivory and disease than found in Puerto Rico (Myster, 2002), and one possible explanation is that *Cecropia* spp. trees are defended from herbivores by ants on the continent, but not on islands such as Puerto Rico (Putz & Holbrook, 1988). Additional protective factors, such as leaf phenolics and tannins, vary among studies (usually on sites other than landslides) so conclusions about the role of herbivory in succession across regional gradients seem premature, even if there are some similarities in the herbivores found on landslides on islands and continents (Myster, 1994).

5.2.6 Non-native species

Typical non-native invaders of landslides have small seeds, are wind-dispersed, and reproduce rapidly. Such r-selected species include grasses, ferns, plants in the Asteraceae, and other small-seeded species; they also tolerate temperature and moisture stress (see Chapter 4) and sometimes spread via rhizomes or stolons (Lundgren, 1978; Francescato & Scotton, 1999). Succession can be altered by the colonization of non-native species in a variety of ways (Prach & Walker, 2011). A few of the potential effects of non-native species include the creation of novel communities, alteration of ecosystem structure and function, inhibition or facilitation of native species, and the arresting or diverting of successional trajectories. A successional framework provides a useful template within which to study the effects of non-native species (Meiners *et al.*, 2007), including the consequences of their eradication or control. Novel communities (Hobbs *et al.*, 2009) make it more difficult to predict the outcome of succession because they are poorly understood but potentially critical in determining successional trajectories. Disturbance is not always a good predictor of non-native invasions (Moles *et al.*, 2012). Non-native species can alter

ecosystem properties directly, such as when they introduce a new function like flammability (Hughes *et al.*, 1991; D'Antonio & Vitousek, 1992; Smith *et al.*, 2000) or nitrogen fixation (Vitousek & Walker, 1989). Nonnative species often alter the relative success of native species, leading to changes in species turnover and diversity (Yurkonis *et al.*, 2005) and these changes, in turn, can alter trajectories and increase divergence. Landslide succession in Jamaica, for example, is altered by the tree *Pittosporum undulatum* (Dalling, 1994) and arrested by the herb *Polygonum chinense* (P. Bellingham, pers. comm.). Alternatively, early successional dominance by non-native species can decline with succession, as reported for landslides in New Zealand (Smale *et al.*, 1997). Despite the rapid increase in studies of non-native species, the effects of landslide disturbances on invasions have not been well studied.

The mixtures of native and non-native species that disperse to and colonize new landslide surfaces generally reflect the surrounding biota. For example, landslides that are in the center of large reserves where native species prevail (e.g., in the Azores; Elias & Dias, 2009) are much less likely to be colonized by non-native species because of the great distances to non-native propagule sources. In contrast, dispersal of nonnatives is facilitated by human-altered landscapes such as farms, villages, and roads. Non-native plants, such as the forb *Desmodium nicaraguensis* and the grass *Hyparrhenia rufa*, were abundant on the large landslide on Casita Volcano, Nicaragua, where farms and villages were intermixed with forest (Velázquez & Gómez-Sal, 2007). Where farmland had fragmented remaining forest in Tanzania, Africa, non-native shrubs (e.g., *Lantana trifolia*), trees (e.g., *Acacia mearnsii* and *Eucalyptus maidenii*), and crop plants (*Sorghum vulgare* and *Phaseolus vulgaris*) colonized 1–7 year old landslides (Lundgren, 1978). Similarly, roads increased the spread of non-native plant species to landslides in the Cascade Mountains of Oregon (Parendes & Jones, 2000) and facilitated landslide colonization by *Miconia calvescens*, which is one of the most problematic non-native plants on Tahiti and other Pacific islands (Meyer & Florence, 1996). Additional disturbances, such as cyclones, can also facilitate the spread of non-native species in tropical forests (Bellingham *et al.*, 2005; Murphy *et al.*, 2008). For example, in the Blue Mountains of Jamaica, Hurricane Gilbert triggered the spread of *Pittosporum undulatum* throughout the forest (Bellingham *et al.*, 2005) and landslides (Dalling, 1994).

Landslides alter ecosystem conditions by damaging or destroying native communities and their seed banks; by exposing low-nutrient, often unstable soils; and by altering competitive balances among native and

non-native communities (Willmott, 1984). These altered conditions can favor invasion by non-native species (Restrepo *et al.*, 2003) and sometimes lead to shallow-rooted plant communities, which could possibly increase the frequency of landslides and abundance of non-natives (Miles *et al.*, 1984; Meyer, 1996). However, more evidence of the effects of variable root structure on slope stability is needed (Stokes *et al.*, 2009). Fire-promoting, non-native invaders of landslides are also likely to promote an increase in fire frequency and reduce long-term slope stability (see Section 5.2.3; Chapter 6).

The Hawaiian Islands are a hotspot for non-native species invasions and they contain among the largest numbers of non-native species of all Pacific Islands (Denslow *et al.*, 2009). The Hawaiian flora now has more non-native plant species that have naturalized than native species, which is in part a result of the relatively recent geological and biological development on very isolated islands (Wagner *et al.*, 1999). The number of non-native seedlings that invaded landslides in Hawaii outnumbered native species invasions both in numbers of species (14 vs. 6) and individuals (895 vs. 322) (Restrepo & Vitousek, 2001). Furthermore, removal of non-native grasses and orchids from landslides resulted in the recruitment of additional non-native plants, which included some species previously unrecorded on the landslides (Restrepo & Vitousek, 2001).

On Hawaiian landslides, a non-native tree fern (*Sphaeropteris cooperi*) from Australia out-competes native tree ferns (*Cibotium glaucum*; Fig. 5.10). *Sphaeropteris cooperi* grows faster, produces more leaves, and retains its leaves longer than does *C. glaucum;* leaves of *S. cooperi* are also faster to decompose than *C. glaucum*, more shade tolerant, and have higher nitrogen and phosphorus content than *C. glaucum* leaves (Durand & Goldstein, 2001a; Allison & Vitousek, 2004; Amatangelo & Vitousek, 2009). These traits allow *S. cooperi* to colonize not only landslides but intact rainforests as well, and the higher nitrogen content of *S. cooperi* potentially increases rates of nitrogen cycling (Durand & Goldstein, 2001b). Experiments suggest that *S. cooperi* leaf litter differentially facilitates growth and nutrient status of some native species under controlled conditions, but its net effect under field conditions is likely to be inhibitory for most native species (Chau *et al.*, in press). Tree ferns are not the only non-natives altering landslide succession in Hawaii. Experimental removal of non-native species of grasses and orchids on landslides on the island of Hawaii led to improved recruitment and growth of the dominant native tree (*Metrosideros polymorpha*), and, in some cases, to invasion by other non-natives (e.g., *Rubus argutus*,

Fig. 5.10. The invasive tree fern *Sphaeropteris cooperi* in Hawaii (canopy) and native tree fern *Cibotium glaucum* (understory). Photograph by M. Chau.

Epilobium ciliatum; Restrepo & Vitousek, 2001). Clearly, non-native plants can be an important component of landslides in both temperate and tropical locations. Knowledge of the level of disturbance and the types of species that comprise the matrix surrounding a landslide can help predict

non-native species invasions on landslides. Due to the high frequency of human visitation to erosion-prone mountain environments, future landslide plant communities will likely be novel mixtures of native and non-native species, perhaps with novel successional trajectories.

5.2.7 Trajectories

Multiple successional trajectories on landslides result from the sum of the complex factors that drive landslide succession. Landslides are among the most heterogeneous of surfaces on which primary succession occurs (Walker *et al.*, 2009). The initial conditions can include a range of sub-strate conditions, from exposed bedrock to patches of intact remnant soil. Soil remnants often contain their original complement of plants and animals (biological legacy; Dalling, 1994; Senneset, 1996). The role of these legacies can be pivotal in determining initial colonists and subsequent species transitions (Shiels *et al.*, 2008), or have little influence if the survivors of the pre-landslide biota fail to colonize the more eroded patches of the landslide (Walker *et al.*, 1996). Legacy effects are most strongly noted in the lower deposition zone, where original pools of seeds and vegetative propagules are supplemented by additions from the upper landslide erosion. Velázquez & Gómez-Sal (2008) noted that succession in the deposition zone of a Nicaraguan landslide was dominated by fast-growing tropical trees, while slower colonization occurred in the upper landslide where soil fertility and instability limited colonization. Trees also typically dominate the deposition zone of temperate landslides (see Fig. 4.7; Flaccus, 1959; Miles & Swanson, 1986). Initial substrate heterogeneity is further complicated by secondary erosion, which can introduce patches of fertile soil into a relatively infertile habitat (see Section 3.3.2). Additional heterogeneity is introduced by litter addition from surrounding vegetation, variable shading, and uneven dispersal of propagules. Propagule dispersal and successful colonization of favorable microsites is still a very poorly understood process (Walker *et al.*, 2009). Thus, the trajectories of succession among several landslides often diverge (Fig. 5.11). Myster & Walker (1997) examined successional trajectories on 16 landslides in Puerto Rico over a period of 5 years and found little convergence of pathways among landslides or between landslides and surrounding forest vegetation (Fig. 5.12). Part of that variation was likely due to differences in soil type, elevation, aspect, and other physical features (Shiels *et al.*, 2008; Shiels & Walker, in press). There were tendencies toward increased shade tolerance following initial soil stabilization;
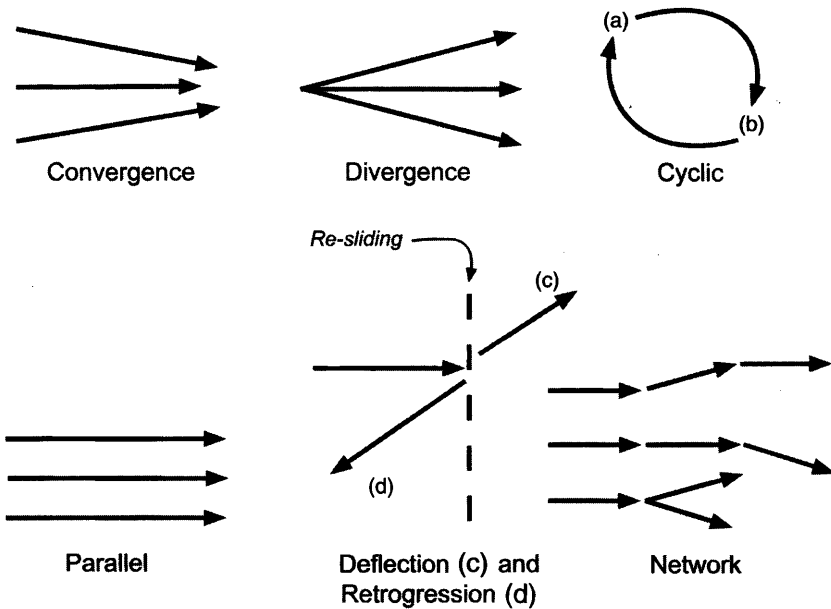
Fig. 5.11. Successional trajectories. Cyclic succession can involve two or more communities (e.g., (a), (b)). Re-sliding can lead to divergence (c) or retrogression (d). Networks can have multiple stable states. Modified from Walker & del Moral (2003) with permission from Cambridge University Press.

soil nutrient availability and local seed availability were also important determinants of landslide successional trajectories. In contrast, Zarin & Johnson (1995b) did find some convergence of soil nitrogen, phosphorus, potassium, and magnesium values in adjacent mature forests within 55 years on Puerto Rican landslides (but much slower recovery of carbon and calcium); Dalling (1994) found slower responses on Jamaican landslides, with estimates of 500 years for convergence to pre-disturbance levels of above-ground biomass.

In addition to convergence and divergence, successional trajectories can be cyclic, parallel, diverted, networked, or retrogressive (Fig. 5.11; Walker & del Moral, 2003). First, landslides can undergo cyclic succession when there are several stages that are replaced in a regular pattern (Elias & Dias, 2009). Landslides in Bolivia that are dominated initially and later in succession by scrambling ferns represent cyclic aspects of vegetative cover (see Section 5.2.3; Kessler, 1999), although total species composition varied substantially. Second, parallel development was shown by Myster & Walker (1997), where total species composition developed
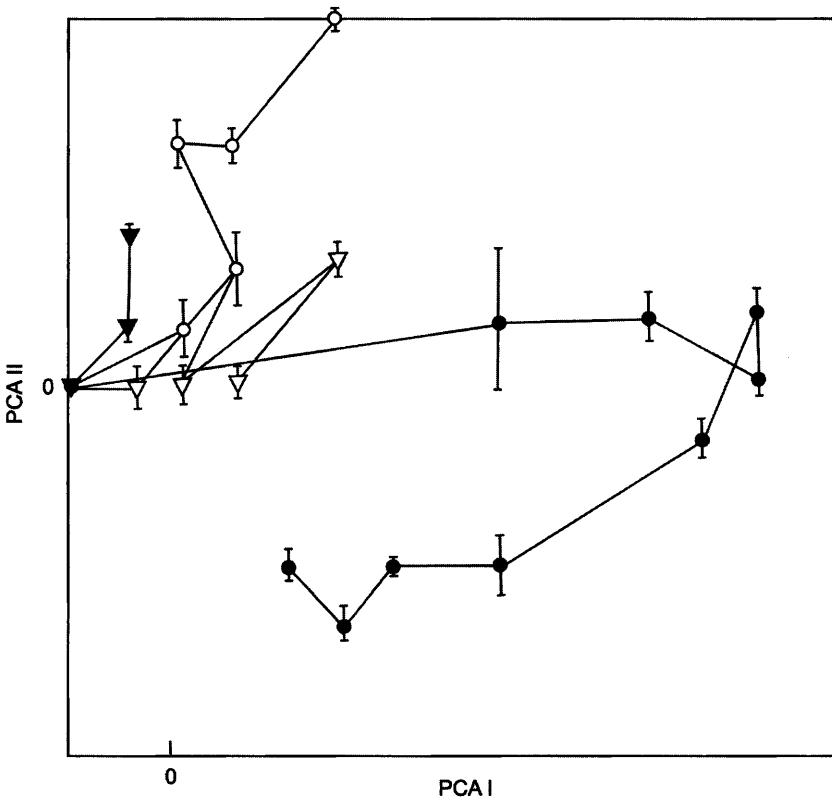
Fig. 5.12. Successional pathways for four Puerto Rican landslides (denoted by four different types of symbols) starting at the same left-most point on the graph. Each point is the average PCA score (coordinate) for all plots sampled for a given landslide at a given sampling date. Modified from Myster & Walker (1997) with permission from Cambridge University Press.

in a similar pattern on some of their 16 Puerto Rican landslides and most plots were dominated by the same common species. In northern Canada, landslides in three areas followed parallel trajectories of vegetation development, although warmer inland locations were more favorable to growth (Cannone *et al.*, 2010). Third, diverted successional trajectories are most common on landslides where secondary disturbances such as erosion (Shimokawa, 1984) and fire (Velázquez & Gómez-Sal, 2007, 2009b) occur and the stochastic nature of early succession results in a new community. This trajectory is particularly likely where non-native species are newly established in the perimeter of the landslide

and are able to compete with the traditional colonists (e.g., *Sphaeropteris* on Hawaiian landslides). Fourth, networks are complex trajectories with multiple pathways. For example, landslides can be dominated for decades by forbs, scrambling ferns, or tree ferns in Puerto Rico (Walker *et al.*, 2010a) and elsewhere (Slocum *et al.*, 2004), giving rise to multiple stable states (Suding & Hobbs, 2009b). Finally, retrogression occurs when carbon and nutrient accumulations cease and begin to decline. This pattern occurs in late stages of succession, often after thousands of years (Wardle *et al.*, 2004; Peltzer *et al.*, 2010), but can occur at much shorter scales and even cycle with periods of progressive succession (increase in carbon or nutrients) at decadal scales (Walker & del Moral, 2009). On landslides, re-sliding (see Chapter 3; Walker & Shiels, 2008; Elias & Dias, 2009), particularly after a period of carbon and nutrient accumulation, can be considered a form of retrogression. On Japanese landslides, re-sliding occurred with sufficient frequency to deter the growth of mature forests (Nakamura, 1984; Shimokawa, 1984).

The study of successional trajectories can be direct or indirect. Direct measures of change involve repeated measurements over many years and are feasible only where there is a long-term research program or very dedicated individuals. Therefore, most measurements of landslide succession are done using chronosequences that involve a space-for-time substitution (Pickett, 1989). Sites of different age are assumed to represent a sequence of development, where the older sites went through the successional stages currently represented by the younger stages. Given the lack of predictability and frequent divergence of landslide seres, the chronosequence approach can be problematic (Johnson & Miyanishi, 2008). The best use of the chronosequence approach is when there is good evidence of temporal links among the stages (Fastie, 1995). These links can be established through aerial photos, presence of transition vegetation, tree rings, lichen growth, fossils, pollen cores, changes in soil depth, carbon isotope ratios, and other techniques (Nott, 2006; Walker *et al.*, 2010b). Bull and colleagues (Bull & Brandon, 1998; Bull, 2010) dated the ages of New Zealand landslides (rock falls) to within about 5 years by using lichen dating. Spatial patterns of rocks of a certain age were then used to create seismic maps. Some parameters (species richness, cover, vegetation structure, and soil organic matter accumulation) are more likely than others (e.g., species abundance and composition) to show convergence and therefore are appropriate to measure in chronosequence studies (Walker *et al.*, 2010b). For the study of millennial-scale changes in vegetation and soil development on landslides, chronosequences are

the best available tool. Multiple short-term processes (e.g., nutrient pools, microbial biomass) are often predictable within the longer chrono- sequence framework (Chapin *et al.*, 2003; Bardgett *et al.*, 2005).

5.3 Temporal dynamics at landscape scales

The spatial heterogeneity that landslides contribute to landscapes (see Section 2.3) is not a static phenomenon, but one that changes over time as landslides and the matrix of vegetation that they are embedded in undergo succession and are impacted by the regional disturbance regime (Pickett & White, 1985) and longer-term geological forces (Swanson *et al.*, 1988). For example, post-landslide erosion and more extensive re-sliding (see Section 3.3.2) can reset succession, initiating new spatial and temporal patterns. When landslide return intervals are long (e.g., > 200 years), succession can reduce the contrast between the landslide scar and its matrix (Shimokawa, 1984). Moreover, landslides interact with other types of disturbances (e.g., deforestation, Restrepo & Alvarez, 2006; or fire, Walker & Boneta, 1995; Cannon, 2001) that affect a given land-scape to create a disturbance regime. These interactions can alter patterns of landslide occurrence and landslide succession, providing a shifting backdrop that can contribute to the variety of successional trajecto-ries. The sometimes sharp physical gradients both within landslides and across landscapes that contain landslides help generate a variety of biotic responses but these physical drivers are also in flux, albeit at relatively slower turnover rates than biological drivers. For example, successional changes in flora and fauna usually occur more frequently than geological changes such as re-sliding or uplift (see Fig. 2.1). Biotic responses to both geological (e.g., fertile soil patches) and biotic (e.g., competition among colonizers) drivers contribute to an overlay of temporally dynamic patches on a relatively stable geological template (Swanson *et al.*, 1988).

Dispersal is an important determinant of temporal heterogeneity within a landslide (see Chapter 4) because neither its timing nor its end result is easily modeled (Hupp, 1983; Dalling, 1994; Shiels & Walker, 2003). For example, seeds of the pioneer tree *Cecropia schreberiana* can be dispersed to landslides by bats (Wunderle *et al.*, 1987) or survive landslides in situ, germinating when exposed to increased red:far red light ratios (Vázquez-Yanes & Smith, 1982). Similarly, birds may disperse seeds to landslides, but the rate of dispersal is dependent on the presence of perches and on the type of ground cover that may already exist on the landslide (Shiels & Walker, 2003). On two Puerto Rican landslides located only
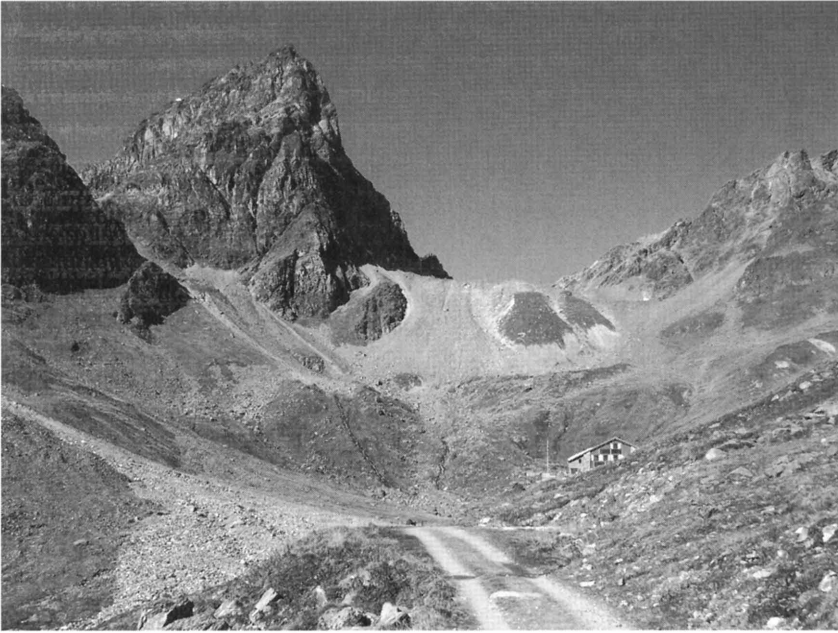
Fig. 5.13. Talus slopes are prominent landscape features in the Swiss Alps. Photograph by B. Cohen.

a few kilometers apart, Walker & Neris (1993) found many different species of wind-dispersed seeds. Such differences have led to different successional outcomes on the two landslides (Myster & Walker, 1997).

Landslides contribute to the physical diversity of landscapes through their influences on topography, soils, and habitats (Table 5.2; Geertsema & Pojar, 2007). For example, topographical changes created by landslides include the formation of cliffs, gullies, ridges, talus, and the damming of rivers and formation of lakes (Fig. 5.13; Schwab, 1983; Cruden *et al.*, 1993; DeLong *et al.*, 1997; Geertsema & Pojar, 2007). Some of these changes can have long-term consequences, as when succession is very slow on exposed talus slopes in New Zealand (Whitehouse, 1982) and new landslides are created before the vegetation recovers (Allen *et al.*, 1999). Landslides also alter soils by exposing new parent material, changing existing soil chemistry, mixing organic and inorganic soils, and creating islands of infertility (e.g., slip faces) and fertility (e.g., rafted vegetation from above the landslide) (Huggett, 1998; Zarin & Johnson, 1995a,b; Butler, 2001). These topographical and soil changes create novel and altered habitats to which the local flora and fauna respond.

Table 5.2. *Physical diversity created by landslides and its ecological consequences, with an emphasis on ecosystems in British Columbia, Canada*

Type of diversity	Type of landslide	Landslide influence	Ecological consequences	References
Site	Many	Scarps and cliffs formed	Increased slope	Geertsema & Pojar, 2007
	Debris flows	Gullies formed	New microhabitats, climates	Schwab, 1983
	Spreads, flows	Hummocks and ridges formed	Drier, warmer than surroundings	DeLong et al., 1997
	Rock slides	Rubble	Increased drainage	Geertsema & Pojar, 2007
	Many	Rivers dammed	Wetter, cooler, new aquatic habitat	Cruden et al., 1993
	Rotational; flows	Lake creation	Wetter, cooler, new aquatic habitat	Geertsema, unpublished observations
Soil	Many	Parent material exposed	Resets soil development	Huggett, 1998
	Many	Change in chemistry	Changes in organic matter and nutrient availability	Lambert, 1972; Geertsema & Schwab, 1995; Zarin & Johnson, 1995a
	Flows	Mix of organic and inorganic	Changes in hydrology, texture, density, porosity; layering of soil types	Butler, 2001
	Translational	Rafted soil and vegetation	Increased heterogeneity	Smith et al., 1986

Habitat			
Rock cliffs	New, steep surfaces formed	Snags, debris for raptors, fish; resets forest succession	Swanson & Franklin, 1992; Geertsema, 1998
Debris flows	Longitudinal variation in sediments	*Betula* spp. on outer, sandy edges; transition to *Picea* on inner cobble	Yajima *et al.*, 1998
Debris flows	Variable habitats	*Alnus* to *Picea* and *Tsuga* except on upper zone (no *Alnus*)	Smith *et al.*, 1986
Debris flows	Gullies formed	*Populus* trees	Lewis, 1998
Rock slides	Talus	Lichens	Bull & Brandon, 1998; Geertsema & Pojar, 2007
Rotational; cliff collapses	Talus	Nest holes for birds	Geertsema & Pojar, 2007
Many	New mineral soil surfaces	Pioneer vegetation supports herbivores including bears	Geertsema & Pojar, 2007
Rock slides	Exposed mineral soil; entrapment of water by rough surfaces	*Populus* outcompetes tundra-grassland vegetation on new surfaces	Lewis, 1998
Rock falls	Covered *Picea* muskeg	*Salix* and *Betula* shrubs invade	Geertsema & Pojar, 2007
Mud flows	Silt exposed; rafted vegetation	Herbs and horsetails; surviving shrubs, sedges, mosses, lichens	Lambert, 1972
Earth flows	Lakes formed	Beavers use dams, lakes, and colonizing vegetation	Geertsema & Pojar, 2007

Modified from Geertsema & Pojar (2007) and references therein.

Regional biodiversity can be maintained by landslides because of the habitat heterogeneity that they contribute to; but locally, landslides often reduce habitat for organisms (Schuster & Highland, 2007). Landslides can denude 1%–2% of forested areas every 100 years in mountainous terrain such as found in Chile (Veblen & Ashton, 1978) or British Columbia, Canada (Smith *et al.*, 1986). However, much larger percentages of the landscape can be affected by disruptions of faults, such as the Alpine Fault in New Zealand (Wells *et al.*, 2001), or when human activities increase landslide frequencies (see Chapter 6). In Chile, old-growth forests were reduced in area by landslides and the fast-growing landslide colonists *Nothofagus* spp. predominated (Veblen *et al.*, 1980). Freshwater organisms can also be affected by landslides through sediment inputs to rivers and lakes. Fish are particularly vulnerable because the sediments can reduce light and therefore algae production, reduce populations of insects and other invertebrates, damage fish gills, and damage spawning grounds (Sidle *et al.*, 1985; Swanston, 1991; Schuster, 2001; Staudacher & Füreder, 2007). Coastal aquatic organisms face similar problems from sediment inputs by landslides; sedentary organisms such as barnacles, clams, and corals do not have the ability to escape high levels of turbidity resulting from up slope landslides (Schuster & Highland, 2007).

Despite their destructive aspects, landslides do provide habitats suitable for colonization by many plants and animals (see Chapter 4). Cliffs provide habitats for birds and rodents (Swanson *et al.*, 1988; Williams *et al.*, 2010) and escape terrain for goats and sheep (Sappington *et al.*, 2007). Debris flows create habitats with variable topography and soil texture. Gullies and ridges provide wetter or drier microhabitats favored by different species. On a debris flow in Japan, tree colonization depended on soil texture, with *Betula* spp. on sand and *Picea glehnii* on cobble (Yajima *et al.*, 1998). The exposed rocks of talus slopes are often colonized by lichens (Kubešová & Chytrý, 2005; Nott, 2006), favor burrowing rodents such as pikas (Millar & Westfall, 2010), and provide some birds with nesting habitat (Sheffield *et al.*, 2006). Exposure or deposition of mineral soil can remove or bury existing vegetation and provide new surfaces that favor colonization of pioneer herbs in tundra (Lambert, 1972) or *Populus tremuloides*, *Betula* spp., or *Salix* spp. trees in taiga (Lewis, 1998; Yajima *et al.*, 1998; Geertsema & Pojar, 2007). Such pioneer vegetation can attract herbivores from rodents to bears, while wolverines and other predators sometimes feed on animals killed in annual snow avalanche chutes in British Columbia (Rozell, 1998). Later successional stages on landslides can provide habitats for organisms that utilize more complex forest

structures, including epiphytes (Kessler, 1999) and monkeys (Kaplan & Moermond, 2000).

Long-term effects of landslide inputs to rivers can be beneficial, particularly when landslides increase habitat complexity by providing large rocks or woody debris to aquatic ecosystems (Sedell et al., 1990). When landslides dam rivers (see Section 2.2.1) and create lakes, forests become flooded, new floodplains are formed, and new erosion and deposition patterns are established. In and adjacent to the newly flooded habitats, floodplain succession is initiated or accelerated, dead snags from drowned trees provide perches for birds, fish obtain new habitats, terrestrial wildlife benefits from new watering holes, and animals like beavers may experience food and habitat improvements (Naiman et al., 1986; Swanson & Franklin, 1992; Geertsema, 1998; del Moral & Walker, 2007). Migratory birds may also benefit from new aquatic habitats resulting from landslides (Amezaga et al., 2002) and fish diversity can increase where gene flow of migratory fish is blocked (e.g., ocean-run trout in the Eel River in California; Mackey et al., 2011). The net effect of landslides on biodiversity is therefore probably beneficial, although not predictably so, especially given the dynamic fluctuations in species composition through colonization and succession. Landslides that increase habitat diversity will most likely increase biodiversity, while large or persistent landslides may decrease both local and regional biodiversity, particularly when they promote dominance by a few aggressive colonists.

5.4 Conclusions

Landslide succession is a dynamic process that is characterized by high spatial heterogeneity, sharp and diffuse abiotic gradients, on-going disturbances, and interactions between abiotic and biotic drivers within landslides, between landslides and their surrounding matrix, and among landslides across a landscape. Spatial heterogeneity contributes to temporal heterogeneity. For example, incomplete or irregular removal of vegetation and topsoil creates differential starting conditions for succession in the slip face, chute, and deposition zones. On-going disturbances within landslide scars include rafting of forest remnants from above, which introduces further temporal heterogeneity in the form of propagules, organic matter, and nutrients. Post-disturbance erosion of landslide edges or unstable soils can disrupt succession in local patches, while more extensive and severe re-sliding can entirely reset succession.

Biotic drivers of plant succession on landslides include stochastic variables such as dispersal, and positive (facilitative), negative (inhibitory), or

neutral interactions among colonists. These interactions can accelerate or inhibit rates of succession. Because a given species can be facilitated and inhibited at different stages of its life cycle, the net effect of all interactions is what ultimately drives succession. Colonizing plant species also affect abiotic conditions including light, soil nutrients, and soil stability. Animals interact with the plant colonists by eating them and dispersing them, or by using the altered habitats; herbivores, pathogens, and non-native species readily alter successional trajectories. Successional trajectories on landslides reflect seres initiated by other types of disturbances, with elements of both convergence and divergence of community properties such as biodiversity. Biodiversity is generally enhanced by landslides because of the increase in habitats in both space and time, which allows colonization by species not found in abundance in undisturbed local habitats.

This chapter has reviewed a number of descriptive and a few experimental studies of terrestrial landslide succession, but there are still many questions that remain. At the scale of individual landslides, humans still do not understand the highly stochastic processes of dispersal and establishment and the interaction of propagules with favorable microsites. We have also not yet explained the role of soil biota in the colonization process, or the influence of early colonists on later ones (priority effects). In addition, surviving organisms and patches of fertile soil (legacies) clearly play an important, but poorly understood role in landslide colonization. Despite much effort, there is still more to determine about how species on landslides interact with each other and how these positive and negative interactions influence successional trajectories. At landscape scales, we need more evaluation of the role of landslide communities in maintaining biodiversity, functional diversity, and carbon and nutrient cycles, particularly in light of increasing influences of humans on landslides (e.g., implications of non-native species; see Chapter 6). For example, are natural landslides more important for biodiversity than anthropogenic ones? Regular, systematic, and standardized observations and experiments will help to address these issues, which are of both theoretical and practical interest (del Moral, 2011). Finally, this chapter has focused on temporal patterns and species interactions on terrestrial landslides, but very little is known about similar processes on submarine landslides (Paull *et al.*, 2005).