

Primary Succession and Ecosystem Rehabilitation

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1 · *Introduction*

1.1 Why learn about primary succession?

This book is for anyone interested in the consequences of disturbance. What happens after the lava cools, or when the muddy floodwaters recede or an old road is abandoned? Primary succession is the process of ecosystem development on barren surfaces where severe disturbances have removed most vestiges of biological activity. It includes the development of complex systems from simple biotic and abiotic (non-biological) components. Primary succession starts when plants, animals and microbes colonize new surfaces. The process is influenced by local conditions, context and site history. All new surfaces are initially devoid of life, so primary succession has been crucial throughout Earth's history. Today, all communities of plants, animals and soils are the result of primary succession. It is this process of recovery of ecosystems after disturbance that provides the clean air and water and fertile soils that humans and all organisms need to survive.

Ecosystem development on initially barren surfaces has always been of great importance to humans. Hunters depended on game that migrated into the fertile terrain exposed by retreating glaciers. With the transition to agriculture, communities became dependent on the periodic deposition of nutrients by floodwaters along such rivers as the Euphrates and Nile to sustain soil fertility and civilization. Away from floodplains, farmers have had to manipulate succession to produce crops on infertile sites. Present-day ecologists use lessons from primary succession in many ways (e.g. to create new habitats and to rehabilitate mined lands and pastures). Effective manipulations of our environment to improve fertility, productivity or diversity and an ability to mitigate undesirable conditions all clearly depend on our ability to understand primary succession. The exponential increase in human numbers and declining resource availability lend great urgency to the search for more efficient resource use and habitat rehabilitation. We hope that this book will provide a comprehensive

understanding of the mechanisms of primary succession that will facilitate that search.

1.1.1 Humans and disturbance

Humans live in awe of disturbances, particularly catastrophes such as floods, earthquakes, hurricanes, meteor strikes and volcanoes that can create the conditions for primary succession. Of course, the terms catastrophe and disaster place a human bias on these natural phenomena. Therefore we will use the neutral and more encompassing term disturbance to refer to disruptions of the environment that trigger primary succession. However, humans are responsible for an increasing array of disturbances such as acid rain, ozone depletion, nuclear explosions and global warming, all of which can exacerbate natural phenomena such as erosion and flooding. Flooding accounts for nearly half of all human deaths associated with such natural disturbances as earthquakes, volcanoes, windstorms, fires and landslides (Abramovitz, 2001). However, the distinction between natural and human-induced disturbances is increasingly blurred because of the growing extent and impact of human activities.

Historical records demonstrate the impact of natural disturbances on human history. Natural disturbances have altered the balance of power in many parts of the world, often by devastating agricultural production and thereby destabilizing societies (Keys, 2000). The eruption of the island of Thera in the Mediterranean Sea in 1623 B.C. (Oliver-Smith & Hoffman, 1999) destroyed the Minoan civilization, thereby changing the course of Western civilization. Global climates were disrupted by gigantic volcanic explosions such as Taupo in New Zealand (A.D. 186), Krakatoa in Indonesia (*c.* A.D. 535 and 1883) and Laki in Iceland (A.D. 1783). We are gaining a better historical understanding of climate change through examination of ice cores in Greenland, deposits from meteor collisions and volcanic debris. Many past disturbances are thought to be responsible for catastrophic extinction episodes. The loss of 90% of all marine species about 250 million years ago during the Permian extinction coincided with the lowering of sea levels and the merging of the continents to form a super-continent called Pangaea. The cooling of the oceans about 65 million years ago marked the end of the Cretaceous and was almost certainly the result of a large meteor impact off the Yucatan Peninsula (Mexico). This impact may have caused the loss of 50% of all marine species and terrestrial organisms, including most dinosaurs. More recently,

the loss of many large mammal species from North America during the Late Pleistocene was associated not only with human hunting pressures, but also with climate warming and a resultant loss of grassland habitat that was replaced by forests.

With a rapidly growing human population that is increasingly resource-hungry, we have entered a new era of intense human impacts on the planet with no clear outcome in sight. Humans disturb life in ways that are unique in the history of the Earth. Because of growing data on ozone depletion and global warming, concerns about global climate change have gained a new urgency. Global warming will lead to higher ocean levels, extensive coastal flooding and destruction of coastal habitats (e.g. marshes, swamps and mangrove forests), increased hurricane frequency and intensity, accelerated desertification and possible human-triggered disruptions of La Niña and El Niño climatic cycles. To counteract this unprecedented onslaught we must understand the mechanisms of repair. Fortunately, the same communication network that brings us daily reports of disturbances around the globe also has encouraged a globalization of responses to disturbance and an awareness of broader patterns (Holling, 1994; Oliver-Smith & Hoffman, 1999). International responses to disturbances include famine relief and various summits on environmental issues (Stockholm, 1972; Montreal, 1987; Rio de Janeiro, 1992), climate change (Kyoto, 1997; The Hague, 2000), or population issues (Cairo, 1994).

Human responses to disturbance vary with the scale, nature and severity of the disturbance as well as with the cultural context (Barrow, 1999). Abrupt and catastrophic disturbances are best remembered. Having a volcano such as Parícutin emerge in your back yard – as one Mexican farmer experienced in 1943 (Scarth, 1999) – is more memorable than the gradual increase in atmospheric carbon dioxide over the past century. In addition, our ability to perceive ameliorative measures decreases with distance from home, size and duration of the disturbance. Sudden, but somewhat predictable, disturbances such as hurricanes, volcanoes or earthquakes can be planned for. Gradual disturbances (e.g. the loss of Mediterranean forests and soil degradation from centuries of farming, grazing and forestry), develop almost without notice and are accepted as normal – at least until some threshold is crossed (e.g. soils erode in a storm). New types of disturbance (atomic fallout, acid rain) are often poorly understood and unforeseen until the damage is well advanced. Risk assessment is a recent approach that provides early warnings of disturbances that affect humans. Unfortunately, humans are all too willing

to settle in areas prone to natural hazards, such as floodplains, hurricane belts and earthquake faults.

Human responses to disturbance are also influenced by the predominant culture. Extreme events displace humans and alter human immigration into the affected area as far into the future as primary succession proceeds. Low-density agrarian cultures are perhaps most resilient (e.g. farmers in Peru after the 1970 earthquake; Oliver-Smith & Hoffman, 1999) because they are relatively self-reliant. If the disturbance is ephemeral (unlike the years of ash fall on Iceland from the volcano Laki that led to mass starvation in 1783), crops can be replanted and cultural necessities re-established. High-density populations may recover rapidly if the people are affluent (e.g. Northridge, California, U.S.A., earthquake in 1994; Bolin & Stanford, 1999), or more slowly when they are poor (e.g. gas explosion in Bhopal, India, in 1984; Rajan, 1999). High-density populations are much more vulnerable than low-density populations because of their dependence on complex physical and cultural infrastructures. Given that more than half of all humans now live in rapidly expanding urban areas, vulnerability to natural or human-induced disturbances will continue to increase.

Humans often migrate to avoid the consequences of natural disturbances. They also may try to endure by changes in diet or behavior. Residents on the slopes of the chronically erupting Japanese volcano Sakurajima all have small concrete shelters by their homes for protection from air-borne volcanic debris (tephra). People may also try to prevent disturbance or ameliorate its effects, as when residents of Heimaey, Iceland, stopped lava from filling their harbor by spraying the lava with sea water (Jónsson & Matthíasson, 1993). Finally, humans may take advantage of the benefits of a disturbance, including the development of new fertile soils. Central American cultures have made use of the ash from Ilopango (A.D. 260) and other volcanoes (depending on the size of the eruption, the depth and acidity of the ash, weathering rates and societal complexity; Sheets, 1999) because volcanic ash is good for soils. Many forms of lava also weather to produce fertile soils suitable for agriculture. The windward slopes of Mount Etna (Sicily) support productive citrus orchards and vineyards, despite millennia of agriculture. Similar benefits come from nutrient-rich sediments that are deposited on floodplains or nutrients released from organic soils by fires. Disturbances can also lead to more governmental aid to build or rebuild infrastructures or increased tourism in areas of dramatic or scenic value (e.g. Mount St. Helens and Kilauea volcanoes, U.S.A.).

Some cultures have therefore adapted to the benefits provided by some disturbances.

1.1.2 Human interest in ecosystem recovery

Humans may be in awe of natural disturbances but we also depend on natural processes that permit recovery of ‘ecosystem services’ (Daily, 1997). These services include the tangible benefits of croplands, game populations, clean air and a dependable water supply, but also such intangible benefits as esthetic spaces, employment and a familiar landscape that are critical to our feelings of well-being and a sense of place (Gallagher, 1993). These very personal issues are additional reasons for learning about ecosystem recovery.

Humans also have intellectual interests in the recovery of ecosystems. The urge to preserve rare species or habitats is driven both by the desire for stable and familiar surroundings and by esthetic, moral or socially conscious motives. Accelerated rates of species extinction and the loss of species and habitat diversity through the homogenizing influence of invasive species motivate some to preserve the familiar or historical species and landscapes. Habitat rehabilitation (e.g. of abandoned roads for wildlife corridors) usually requires knowledge about the process of primary succession. Large-scale, futuristic habitat modifications such as mariculture (e.g. growing crops of algae on glass plates suspended in the ocean) or terraforming the moon or Mars will certainly be based on the principles of primary succession. Such activities – at any scale – will become an increasing part of our global economy.

Preservation or rehabilitation of ecosystem services following a disturbance can have positive influences. For example, a hurricane may directly reduce crop production through flooding or indirectly reduce visits by tourists. Both consequences disrupt the local economy but efforts to restore crops and revive tourism can stimulate economic development. In the growing field of ecological economics, resources are assigned values, the maintenance of which is dependent on the intricate interactions of ecological processes, including recovery following disturbance.

1.2 Definitions

We define several important terms in this section. Other terms are introduced as they arise or are included in the glossary. Succession is most simply defined as species change over time (turnover). Such a

process is readily observed in many ecosystems, but may be less obvious or even non-existent in stressful environments such as deserts or tundra. We adopt this broad definition for its wide applicability. Yet there is value in contrasting the rich variety of types and trajectories of succession (see Chapter 7).

Temporal changes in the characteristics of an ecosystem (nutrients, biomass, productivity), a community (species diversity, vegetation structure, herbivory) or a population (sex ratios, age distributions, life history patterns) are closely associated with species change. Therefore, succession is sometimes measured by these variables (Glenn-Lewin & van der Maarel, 1992). Time intervals are best measured in relation to the species involved, often one to ten times the life span of the species. Thus, succession of microbes occurs in hours, fruit flies in weeks, grasses in decades and trees in centuries. Historical reconstructions of very long-term changes (paleoecology) and fluctuations around a relatively stable community (seasonal patterns) are generally excluded from studies of succession.

Succession also occurs over a wide range of spatial scales, again linked to the relative size of the organisms of interest. Microsite variations (e.g. in pH or nutrient availability) can be vital for soil organisms (see section 4.4 on soil biota) or annual plants, whereas some processes such as long-distance seed dispersal (see section 5.3 on dispersal) are best measured on landscape scales. Patch dynamics (Pickett & White, 1985; Pickett *et al.*, 1999; White & Jentsch, 2001) incorporate spatial patterns and shifting patterns of areas with similar characteristics across the landscape and have many implications for succession (see section 2.1.4).

Studies of succession have followed both holistic and reductionistic approaches (see Chapter 3). The former approach, espoused by Clements (1916) and some modern-day ecosystem scientists (Odum, 1969, 1992; Margalef, 1968a,b) views succession as linear and directional, ending in a final species equilibrium or climax. This innately satisfying concept – that succession has a direction with a predictable endpoint – has been widely challenged, beginning with Gleason (1917, 1926) and further elaborated by Egler (1954), Drury & Nisbet (1973) and Whittaker (1974). The more commonly held view now (and the one we espouse in this book) is that succession is a process of change that is not always linear and rarely reaches equilibrium. Directionality occurs only in the sense that there is a turnover in the species present, not in the sense of heading toward a known or predictable endpoint. Succession can therefore incorporate multiple types of trajectory including ones that are cyclic, convergent, divergent, parallel or reticulate (see Chapter 7). Disturbance

often redirects or resets successional trajectories, leading to the observation that stable endpoints are rarely achieved. However, disturbances are not evenly distributed in time or space, so the landscape becomes a mosaic of patches, each at a different stage of successional development (Pickett & White, 1985). Rates of successional change also can vary among patches, depending on local site factors such as soil fertility and the mechanisms that regulate the change. To confound the issue, there are multiple mechanisms that drive species change within any given sere (a sere is a particular successional sequence) (Walker & Chapin, 1987). Such complexity has been appreciated for over a century and led Cowles (1901) to suggest that succession was a ‘variable approaching a variable rather than a constant.’ It is not surprising, then, that no agreement has been reached on the definition of succession. Some plant ecologists have suggested that because the term succession is loaded with connotations of directionality and equilibrium, the term vegetation dynamics is preferable (Miles, 1979, 1987; Burrows, 1990). However, we have no trouble using the term succession, because it has a broadly accepted general meaning of species change over time. Further, vegetation dynamics does not always refer to processes of species turnover. We caution, however, that the term should be carefully defined for each usage by specifying both temporal and spatial scales of interest. For example, dividing types of succession into increasingly longer time scales (Glenn-Lewin & van der Maarel, 1992), one might distinguish among fluctuations, fine-scale gap dynamics, patch dynamics, cyclic succession, secondary succession, primary succession and secular succession (i.e. changes due to climatic change or those measured by paleoecology).

Disturbance starts, directs and may stop or redirect succession (see Chapters 2 and 7), so an understanding of its complexities is critical to interpreting successional pathways. Disturbance and succession are both broad terms, difficult to define precisely, yet unavoidably crucial when interpreting temporal change. Disturbance and succession are also strongly interactive, although Grubb (1988) points out that succession and disturbance are not invariably coupled. Disturbance is an event that is relatively discrete in time and space and one that alters population, community or ecosystem structure. As with succession, the exact temporal and spatial scales of the components of interest need to be defined. Disturbance is characterized by its frequency, extent and magnitude (see Chapter 2).

Primary succession involves species change on substrates with little or no biological legacy, that is, substrates that have no surviving plants, animals or soil microbes. Secondary succession begins with some biological

legacy (Franklin *et al.*, 1985) following an initial disturbance (e.g. intact soils). Primary and secondary succession are not always clearly distinguishable, but are points on a continuum (Vitousek & Walker, 1987; White & Jentsch, 2001) from ecosystem development on sterile substrates (lava) or near-sterile substrates (glacial moraines) to development on well-established soils following fire, forest clear-cutting or abandonment of agricultural lands. Regeneration dynamics is a term used to describe one endpoint of the continuum, where there is damage but no mortality (e.g. only loss of leaves and branches of trees during a hurricane).

Secondary succession on low-nutrient substrates can resemble primary succession on fertile substrates (Gleeson & Tilman, 1990). There are numerous examples that are difficult to categorize as either primary or secondary succession. For example, volcanic lava clearly buries soil and biota, but the effects of volcanic tephra depend on the depth of deposition following the eruption. Shallow layers of tephra may cause only minor damage to leaves or understory plants (Grishin *et al.*, 1996; Zobel & Antos, 1997). Similarly, differential depths of burial by sand, floods or landslides can result in secondary or primary succession. And what about burial by plant matter such as wrack (seaweed or other sea life cast onto the shore; Pennings & Richards, 1998)? We take an inclusive approach in this book, utilizing examples that illustrate our themes whether or not they are primary succession in the strictest sense. Further, we de-emphasize the source of the disturbance because different disturbances can have similar results. For example, many disturbances (e.g. glacial melt waters, volcanoes, earthquakes, road construction, heavy rains or mining activities) can trigger landslides. Yet succession results from the conditions created by many, often interacting disturbances, so an understanding of the disturbance regime is essential. We emphasize the actual site conditions that are the net result of the disturbance regime, including the initial status of soil development. Carefully following soil development over time makes a fascinating study in primary succession where most processes have to start *de novo* (see Chapter 4). Yet too little is known about soil development in primary succession to make robust predictions about successional trajectories.

Autogenic succession occurs when the mechanisms that drive species change are derived from the organisms within the community (e.g. nurse plant effects or competition). Allogenic succession occurs when abiotic forces (generally outside the system) determine species change (e.g. sediment transport from a flood, ash deposition from a volcano). Species change in the early stages of primary succession is due mostly to allogenic

mechanisms, but internal, autogenic mechanisms become more important as succession proceeds (Matthews, 1992). However, as with most dichotomies (cf. primary and secondary succession), autogenic and allogenic succession represent endpoints of a continuum. Any given sere is the consequence of a mixture of both mechanisms and it is unwise and naïve to label an entire sere as either autogenic or allogenic (Glenn-Lewin & van der Maarel, 1992).

1.3 Methods

The study of succession involves various techniques adapted to a wide range of temporal and spatial scales (Fig. 1.1). Direct observation of temporal change on permanent plots is best (Fig. 1.2), especially when combined with experimental manipulations that have un-manipulated controls (Austin, 1981; Prach *et al.*, 1993). Repeat photography is useful for identification of changes in populations of long-lived plants (Hastings & Turner, 1980; Wright & Bunting, 1994; Webb, 1996) and it does not involve maintenance of permanent plots. However, where change is on the order of decades and centuries (and photographic records are not available), scientists must use the indirect chronosequence approach, where plots of different ages are presumed to represent different stages of development in the actual succession. The main disadvantage of this space-for-time substitution is that the older sites have different histories than the younger ones (Pickett, 1989; Fastie, 1995). The differences among sites can have multiple causes including stochastic events, changes in landscape context or climate over time, or initiation of succession during different seasons. All of these causes can affect both species invasions and species interactions, resulting in different successional outcomes (see Chapter 7).

A century of observations of seres has provided a wealth of information about the patterns of species change. However, the mechanisms that drive succession remain poorly understood. Typical mechanisms include such aspects as the accumulation of organic matter, competition and grazing (see Pickett *et al.*, 1987). Experimental manipulations are usually necessary to determine mechanisms. Common approaches in succession experiments include alteration of such resources as nutrients through additions (fertilizer, leaf litter) or removals (sawdust, sugar or other carbon sources that immobilize nutrients). Species can also be manipulated through additions (transplants, seeding) or removals (cutting, uprooting, girdling, herbivore exclosures). However, any manipulation can have

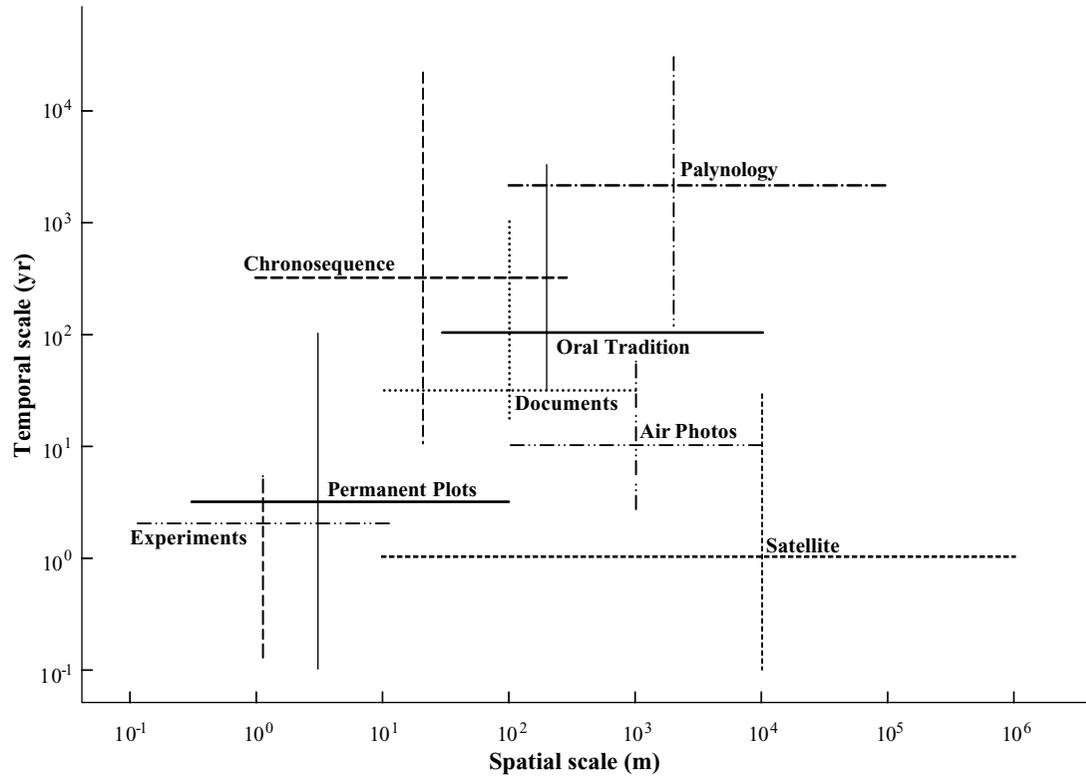


Fig. 1.1. Spatial and temporal scales at which primary succession may be studied. The range of each line is from the finest resolution to the broadest extent normally encountered. The lines cross where the method is most commonly used. Modified from Prentice (1992), with kind permission from Kluwer Academic Publishers.

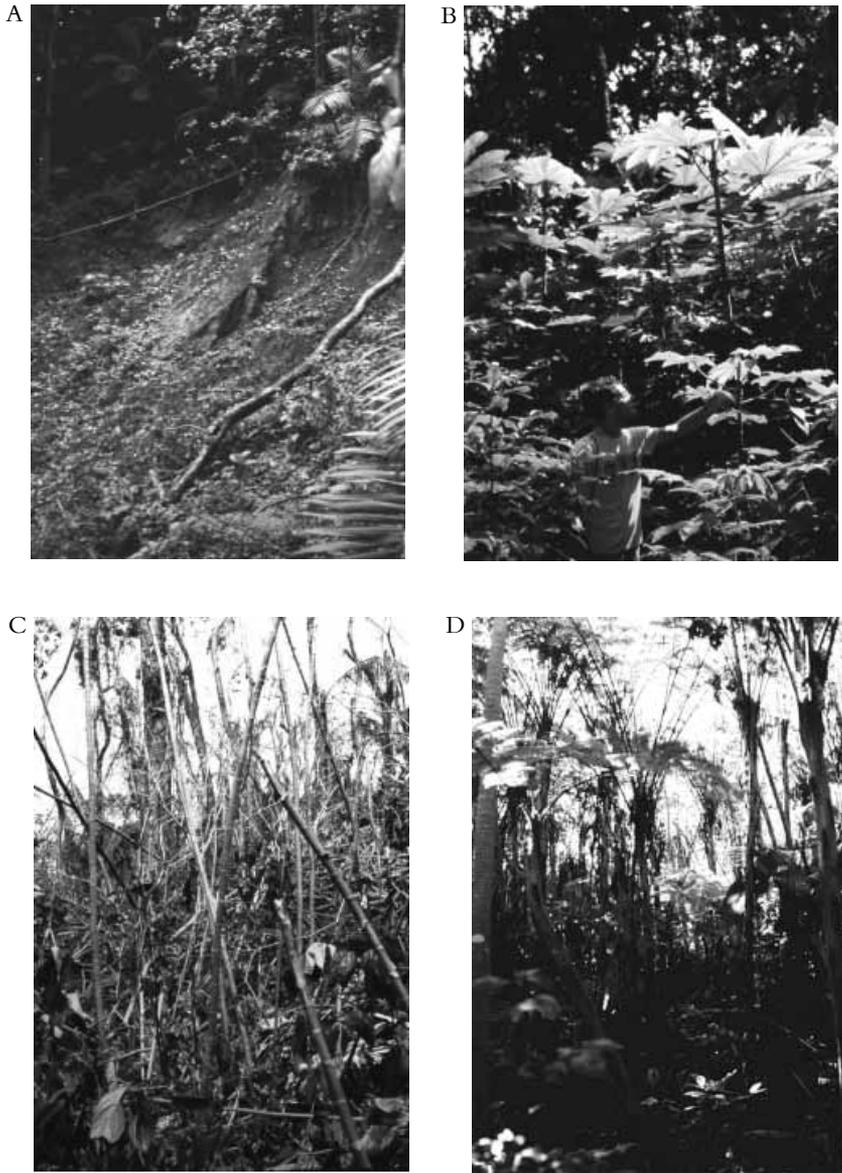


Fig. 1.2. Primary succession on a landslide in Puerto Rico. (A) Initial seedling invasion at 6 mo; (B) *Cecropia* saplings 4 m tall at 18 mo; (C) near total destruction of *Cecropia* saplings from Hurricane Hugo at 22 mo; (D) shift in dominance to *Cyathea* tree ferns that were 10 m tall after 80 mo. Note the unpredictable shift in species composition from a secondary disturbance.

undesirable side effects (Canill *et al.*, 2001). For example, the removal of the aboveground portion of a small tree results in decaying roots in the soil and a vacant spot in the canopy. Ideally, species effects are measured by excluding a target species from the beginning of a sere, rather than abruptly removing (or adding) it in mid-succession. Alternatively, removals and additions in various combinations (and at various stages) can help to clarify which aspects of the target species are influencing succession.

Multivariate analyses (e.g. gradient analyses) or various modeling approaches (see Chapters 3 and 7) can be used to study succession. Further evidence can be obtained from oral histories, historical observations by travelers such as John C. Fremont and geologists and paleoecologists using fossils (Bhiry & Fillion, 1996) or pollen cores (Birks, 1980a). Combining several approaches to studying succession is valuable. Studies of primary succession at Glacier Bay, Alaska, have used Native American legends, reports from the British explorer George Vancouver, detailed observations by geologists, photographs by naturalists, permanent vegetation plots and tree cores (Engstrom, 1995). Most recently, lake-bottom deposits and water chemistry (Engstrom *et al.*, 2000), soil samples and experimental manipulations (Chapin *et al.*, 1994) have helped to understand species change.

1.4 Questions that still remain

It is unclear when primary succession actually ends or is replaced by secondary succession (e.g. succession following a forest fire on a glacial moraine hundreds of years after initial forest establishment). If vegetation change (or any other parameter of interest) is slowed and a relative equilibrium exists for an extended period of time, primary succession can be considered complete (see Chapter 9). However, soil changes may continue long after vegetation change is no longer apparent (see Chapters 4 and 8). We will focus mostly on the dynamic phases of early primary succession but address some of the longer-term changes where data are available from paleoecology (e.g. Jackson *et al.*, 1988) or repeated visits by a series of investigators with long-term plots (e.g. Glacier Bay, Alaska; Cooper, 1931, 1939; Lawrence, 1958; Reiners *et al.*, 1971; Chapin *et al.*, 1994) or without long-term plots (e.g. Krakatau, Indonesia; Treub, 1888; Ernst, 1908; Docters van Leeuwen, 1936; Tagawa *et al.*, 1985; Whittaker *et al.*, 1989).

Another question that remains is the degree to which we can predict successional change. Despite much formal study of succession, no

general theory of succession has emerged that can predict the dynamics of species replacements in many different habitats. The enormous variety of the natural world has confounded attempts to generalize, and successional trajectories are very sensitive to site-specific conditions (see Chapter 7). Comparisons of trajectories at different sites within a habitat or across habitats suggest that pathways may converge when biotic controls are strong and diverge when abiotic factors predominate (Matthews, 1992). Several basic mechanisms have been identified (e.g. competitive inhibition, facilitation; Connell & Slatyer, 1977) that appear to be important drivers of most successional change. We discuss how such species interactions affect succession in Chapter 6. Determining the relative importance of each mechanism and how each is modified by local factors is a first step toward a general theory of succession, even if there will never be a 'grand underlying scheme' (GUS) that explains all successional change. We address such theoretical issues about succession in Chapter 3.

Can studies of primary succession lead to practical generalizations about rehabilitation? Environmental regulations increasingly require polluters and excavators to restore severely damaged habitats such as mined lands or roads to some degree of vegetative cover or ecosystem service (e.g. water retention, erosion control, sediment filtering). Site-specific studies examine ways to manipulate primary succession (either by accelerating it or by holding it at some desirable stage). Comparisons of the results of many such studies can lead to predictions about the rates and trajectories of primary succession on anthropogenic disturbances, provided that the studies are done with proper controls and use repeatable methods. Any valid linkage between specific studies and broader theoretical frameworks can then provide generalizations that can be extremely useful to land managers at other sites to address solutions to their particular problems (Luken, 1990). We argue in Chapter 8 that managers and ecologists have much to learn from each other about rehabilitation.

In writing this book we have three objectives. We want to convey our enthusiasm about the dramatic consequences of disturbance and the excitement in observing and studying how plants and animals return following severe disturbances. We also want to contribute to a practical understanding of how to accelerate reconstruction of damaged systems through the process of identifying the spatial and environmental constraints to ecosystem development. Finally, we present the first organized synthesis of what is known about the patterns and processes of the broad topic of primary succession. We address the frontiers for further research in Chapter 9.