Interactions and Linkages among Ecosystems during Landscape Evolution

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We synthesize our findings of studies in Glacier Bay National Park and Preserve, southeastern Alaska, to elucidate interactions and linkages among terrestrial, lake, stream, and marine intertidal ecosystems as the landscape evolves following ice recession. Development in each ecosystem is initially dominated by physical processes. Over time, biotic control becomes increasingly important, although the extent of biotic control varies among ecosystems. The changes occurring in the four ecosystems are linked by landscape processes, with the nature and strength of these linkages changing through time. Change in one ecosystem has a major influence on the nature and direction of change in other ecosystems. Soil development and woody biomass accumulation on land provide an inertia that is unmatched in stream, lake, or intertidal systems. It is important that researchers and managers understand this science of change, at different spatial and temporal scales, in order to predict future states of ecological systems. The dynamics of change that we document at Glacier Bay during primary succession have important implications for managing the system with respect to anthropogenic change.

Keywords: landscape, development, ecosystems, succession, linkages

One of the most difficult challenges facing ecologists is to understand and predict rapid change in Earth's ecosystems, precipitated by shifts in important drivers. Such drivers include climate; the abundance of key plant and animal species, including exotics; and atmospheric concentrations of carbon (C) and nitrogen (N), two elements that commonly limit ecosystem productivity (Vitousek et al. 1997). Therefore, understanding the science of change is critical to predicting the future state of ecological systems and their services to society. Much of the theory and understanding in ecology, however, comes from ecosystems that are not undergoing rapid change. In these more stable ecosystems, structure and composition do not change radically over the long term, and inputs of energy and materials are approximately equal to outputs. As external drivers change, predicting the response of ecosystems in flux may be more difficult than predicting the response of stable ecosystems.

Ecological studies provide a source of theory and information about ecosystems undergoing change, particularly with respect to secondary succession (Pickett and White 1985, Wallace 2004). Glacier Bay National Park and Preserve in southeastern Alaska (figure 1) provides a unique opportunity to study the primary successional development of newly created ecosystems. Following rapid and well-documented glacial retreats, adjacent terrestrial, lake, stream, and intertidal habitats are exposed to biotic colonization and community development. A suite of largely independent studies conducted in these different ecosystems at Glacier Bay

has shown surprisingly similar patterns of development, characterized by accumulation of organic matter, changes from pioneer species to taxa characteristic of more complex communities, and the development of biotically derived structural features. These patterns suggest a general shift from physical control to increasing biotic control as succession proceeds. For example, as plants cover recently deglaciated surfaces and drive changes in soil development, adjacent young lakes become more acidic, with higher levels of dissolved organic carbon (DOC) and lower concentrations of ions, such as calcium (Ca^{2+}), that have a mineral soil origin (Engstrom et al. 2000). Similarly, in streams, colonization is initially driven by abiotic variables, particularly water temperature and channel stability, which give way to the increased influence of biotic controls as terrestrial vegetation stabilizes stream banks

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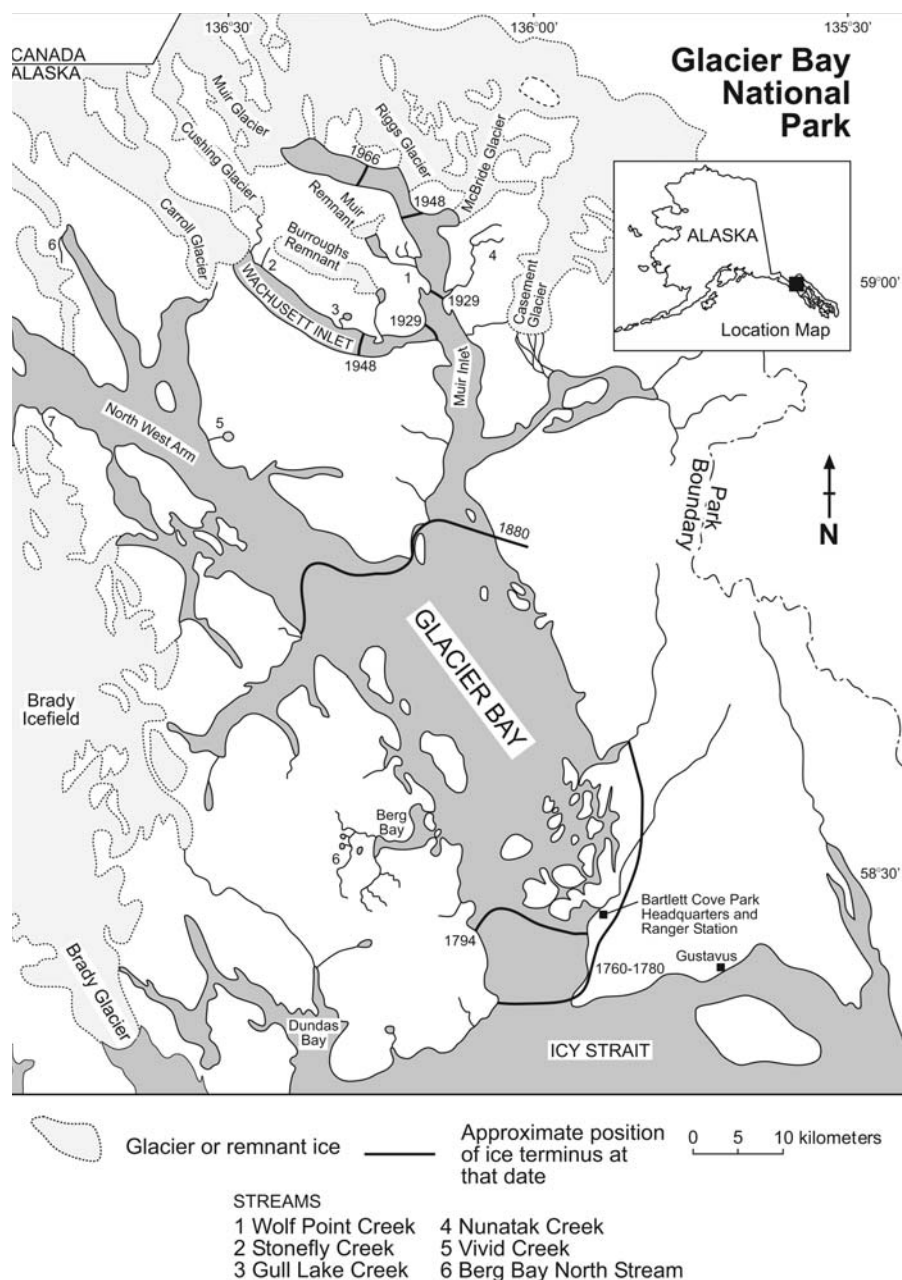
Figure 1. Glacier Bay National Park, showing the key ice recession dates.

physical processes influence biotic colonization, and the rate and extent to which biotic factors play an increasing role. Two important messages emerge from our synthesis: (1) There is a shift from physical control to greater biotic control in all ecosystems, and (2) the changes occurring in different ecosystems are linked by landscape processes (Reiners and Driese 2001, Seastedt et al. 2004), with the nature and strength of these linkages changing through time.

The landscape surrounding Glacier Bay includes glacier-clad mountains up to 5000 meters (m) above sea level, hundreds of kilometers (km) of shoreline, and extensive regions of bedrock and unconsolidated glacial sediments in between. Most studies of ecosystem development at Glacier Bay, including classic studies (e.g., Cooper 1923, Crocker and Major 1955, Lawrence 1979) and studies by the authors of this article, focus on sites within 4 km of the coast and below an elevation of 100 m. The streams, lakes, and terrestrial surfaces studied were formed in unconsolidated glacial deposits that included till and outwash. The successional development of high-elevation, bedrock-dominated, or wetland environments at Glacier Bay has received little scientific attention to date, and our conclusions may not apply to these environments.

A physically controlled landscape (up to five years)

In this section we discuss processes that typically occur in the five years following deglaciation (figure 2a). Since the Neo-glacial maximum in 1750, more than 2600 km^3 of glacial ice has melted within the boundaries of Glacier Bay National Park and Preserve (Larsen et al. 2003). This massive flux of ice accounts for about 80% of the water delivered from land to the ocean during the last 250 years, with the remaining 20% coming from unfrozen precipitation. This glacial recession has exposed Glacier Bay, a 100-km-long fjord, and approximately 1500 km^2 of fresh land surface along its shores (figure 1).

The massive quantities of sediments, ice, and freshwater delivered to the ocean by tidewater glaciers create a marine environment dominated by physical controls. Upwelling driven by cold, low-salinity, nutrient-rich water supports extremely high phytoplankton productivity (Etherington et al. 2004), which in turn supports a complex food web comprising fishes, marine mammals, and seabirds. However, in the

and contributes coarse woody debris (CWD; Milner et al. 2000). Emerging from these studies, which were focused on single ecosystems, is evidence of strong linkages among ecosystems. Similar patterns have been described in terrestrial and intertidal environments (Crocker and Major 1955, Sharman 1989), raising questions about the extent to which these apparent similarities result from separate but similar processes or are linked by landscape interactions.

In this article, we synthesize the major patterns of change in landscapes that include terrestrial, lake, stream, and marine intertidal ecosystems at Glacier Bay, and outline the direction and magnitude of interactions among the four ecosystems with time. These ecosystems differ in the manner in which
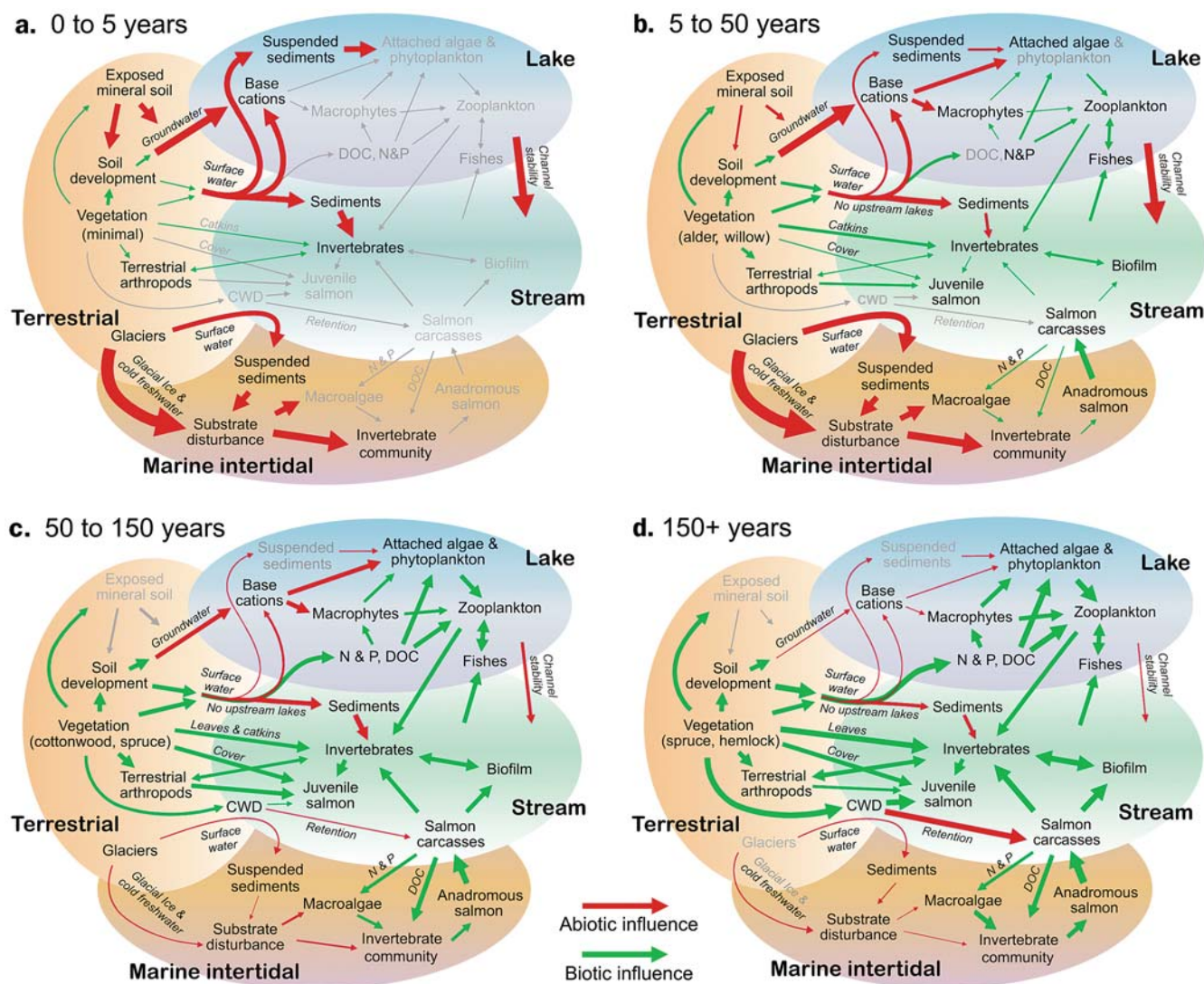
Figure 2. Major linkages among and within stream, lake, terrestrial, and marine intertidal environments at Glacier Bay at four time periods following glacial retreat. The thickness of the arrows indicates the strength of the influence, which may be positive or negative. Red arrows represent abiotic processes; green arrows represent biotic processes. Gray components have little or no importance in the time period shown. Abbreviations: CWD, coarse woody debris; DOC, dissolved organic carbon; N, nitrogen; P, phosphorus.

marine intertidal community, the deposition of silt and the scouring by icebergs limit biotic colonization, resulting in a low-diversity community dominated by filamentous algae and barnacles (Sharman 1989).

With the retreat of glaciers from tidewater, meltwater creates new drainage patterns on land and forms incipient streams and lakes. Remnant ice sheets become isolated in valleys. With no connection to an active glacier and thus no accumulation zone, the remnant ice sheets deliver water and sediments to the ocean through a new set of physically regulated landscape processes. The melting glacial remnants and retreating active glaciers uncover a chaotic mosaic of mounds, ridges, depressions, and debris-covered blocks of ice. As the ice melts, water fills the depressions to form lakes. Because of relatively warm summer temperatures and a gen-

erally thin cover of glacial drift, melt-out of buried ice blocks is usually rapid in the low-elevation forelands of Glacier Bay (Engstrom et al. 2000). Turbid, silt-laden streams flow from the active or remnant ice or proglacial lakes across new terrain to the ocean. These stream channels are unstable and frequently migrate across the landscape, as they erode unconsolidated glacial deposits. These young streams are cold (maximum temperature < 4°C), because much of the water originates from melting ice (Milner et al. 2000). Many of the newly formed lakes and streams are ephemeral features that eventually disappear as the landscape matures.

On terrestrial surfaces, the newly exposed glacial deposits contain variable proportions of carbonate parent material (Ovenshine 1968, Fastie 1995a), and the young soils that develop on them have a high pH (7 to 8) and low cation exchange
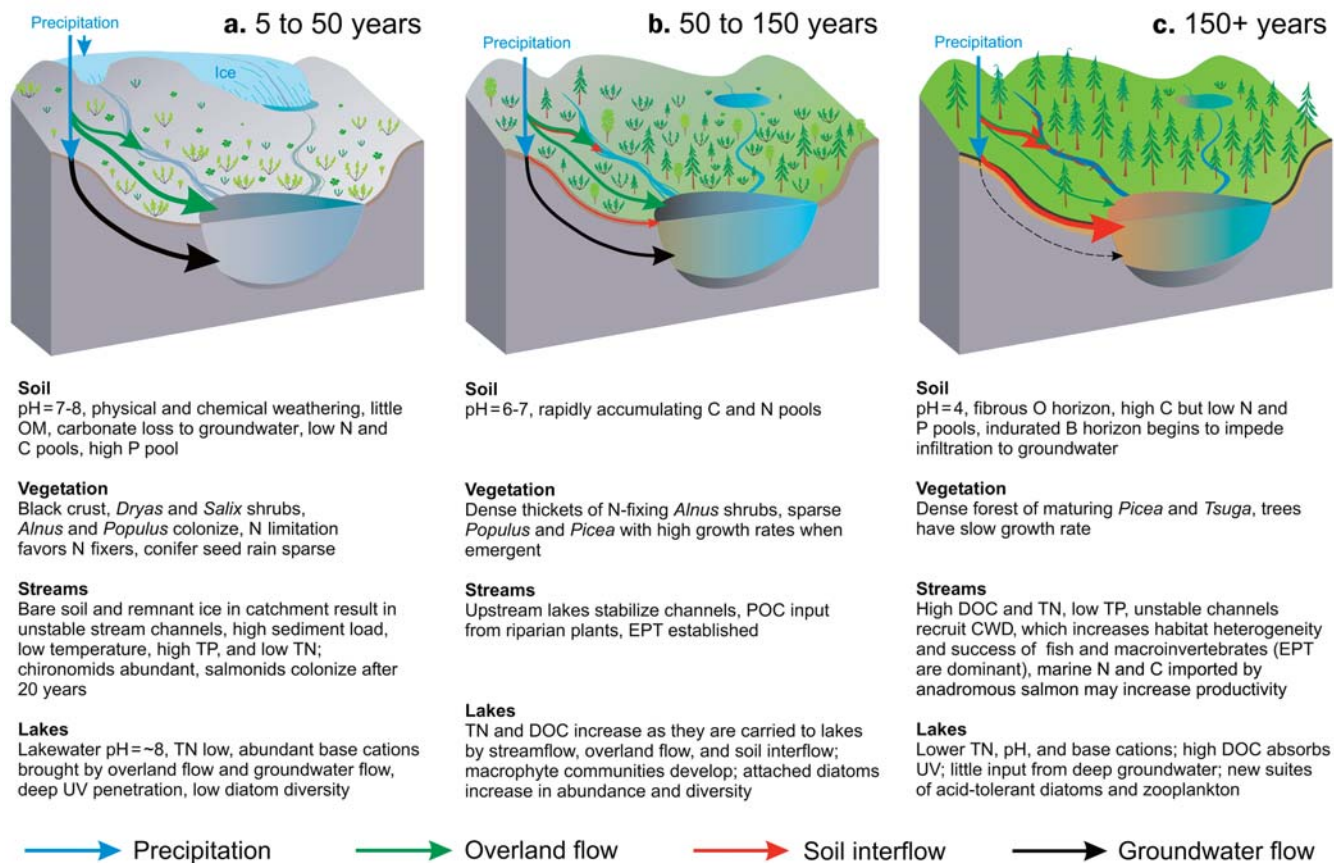
Figure 3. Major features of terrestrial, stream, and lake environments at Glacier Bay at three time periods following glacial retreat. Arrow thickness represents relative contribution to stream and lake water from overland flow, soil interflow, and groundwater flow. The three panels represent different parts of the Glacier Bay landscape and do not constitute a sequence that has been followed at all sites. Abbreviations: C, carbon; CWD, coarse woody debris; DOC, dissolved organic carbon; EPT, Ephemeroptera, Plecoptera, and Trichoptera; N, nitrogen; OM, organic matter; P, phosphorus; POC, particulate organic carbon; TN, total nitrogen; TP, total phosphorus; UV, ultraviolet radiation.

capacity (Crocker and Major 1955, Ugolini 1968, Chapin et al. 1994). The large amounts of mildly acidic precipitation that are typical of the region leach cations (Ca^{2+}, Mg^{2+}) from the upper soil horizons. Near the soil surface, pH declines, iron- and aluminum-rich minerals oxidize, and N from precipitation accumulates slowly. Even as tidewater glaciers retreat onto land, adjacent marine intertidal development is severely constrained locally by physical controls through the continued input of large volumes of cold, fresh, silt-laden water.

Organisms colonize (5 to 50 years)

In this section we discuss processes that typically occur between 5 and 50 years after glaciation (figures 2b, 3a). As the physically controlled dewatering of the landscape proceeds, patches within this landscape mosaic stabilize, although they are still influenced by the microclimate of nearby glacial remnants. Within 5 to 15 years of deglaciation, fine-textured terrestrial sediments are occupied by a community of N-fixing cyanobacteria, bryophytes, gametophytes of the horsetail (*Equisetum variegatum*), and lichens (figure 4; Worley

1973, Lawrence 1979). This "black crust" community stabilizes the soil surface and begins to reduce sediment transfer to streams. These organisms also incorporate C and N from the atmosphere and eventually are converted into soil organic matter as they die. This community reduces germination but increases the survivorship of newly germinated seedlings of vascular plants (Chapin et al. 1994) and at most sites is overtopped by these plants within 30 years. Regardless of species composition, this first community of vascular plants accelerates the transition from complete physical control of landscape processes to significant biotic control.

Once biological communities begin to develop on land, there is a rapid shift in the nature of controls over landscape processes. In fact, at Glacier Bay, the landscape-level biotic process of propagule dispersal influences terrestrial succession as soon as land surfaces are ice free. When the Glacier Bay ice lobe began its catastrophic retreat (ca. 1750), the distal ice margins were adjacent to old-growth forests of western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*), and these communities were the primary source of propagules

arriving on newly exposed surfaces. By 1850, the glacier had retreated 50 km, exposing land more than 20 km from hemlock–spruce forests. Propagules reaching these younger sites came primarily from the advancing front of early-successional vegetation composed of Drummond's mountain-avens (*Dryas drummondii*), willows (*Salix* spp.), and Sitka alder (*Alnus sinuata*). As colonizing vegetation chased the retreating glacier in the 20th century, black cottonwood (*Populus trichocarpa*) became another important colonizer, and its seeds arrived quickly at sites that today are less than 100 years old. Thus the geography of linear glacial retreat at Glacier Bay created dramatic differences in early seed rain to sites exposed at different times. The position of a particular site within the Glacier Bay landscape largely determined which seeds arrived there and therefore which species were prominent in early succession (Fastie 1995a).

The interplay of physical microsite conditions and plant traits determines which of the early-arriving species germinate and establish. At this stage, landscape position and the physical environment are filters that directly exclude most species, favoring those with great dispersal ability and tolerance for exposed sites with low soil resources. However, a decade or two later (two to three decades after exposure), the density of colonizing plants is sufficient for facilitative and competitive interactions to begin to influence community change. For example, *Dryas,* a ground-hugging, N-fixing shrub, reduces the germination of alder and the initial growth of spruce seedlings (Chapin et al. 1994). The *Dryas* mat increases the growth of older spruce seedlings and inhibits the growth of older alder seedlings. When *Dryas* is subsequently overtopped by taller plants, its growth rate is reduced by shading and by apparent allelopathic effects of alder litter (Chapin et al. 1994). By this time, three to five decades after ice retreat, the community is in the later stages of a transition from domination by the dynamics of colonization to domination by species interactions involving resource acquisition. Although competitive and facilitative interactions become increasingly important, the legacy of early filtering of colonizers by landscape position and physical environment persists.

Lake environments follow a pattern of biological development in this young landscape that parallels that of the terrestrial ecosystem (Engstrom et al. 2000, Fritz et al. 2004, Engstrom and Fritz 2006). Newly formed lakes are initially turbid from glacial silts and clays, but quickly clear as ice retreats from the catchment. The water chemistry, reflecting drainage from unweathered soils, is characterized by high pH (7.9 to 8.3) and high cation concentrations, but low N availability. Productivity is consequently very low and is restricted to a few species of attached algae, principally diatoms such as *Gyrosigma spencerii, Amphora perpusilla,* and *Achnanthes minutissima.* The lakes at this stage are typically quite clear, as a result of the lack of inputs of DOC (< 1 milligram [mg] per liter [L]) from the terrestrial environment. Consequently, ultraviolet radiation penetrates to depth, limiting zooplankton assemblages to a handful of early colonizers (e.g., *Cyclops*
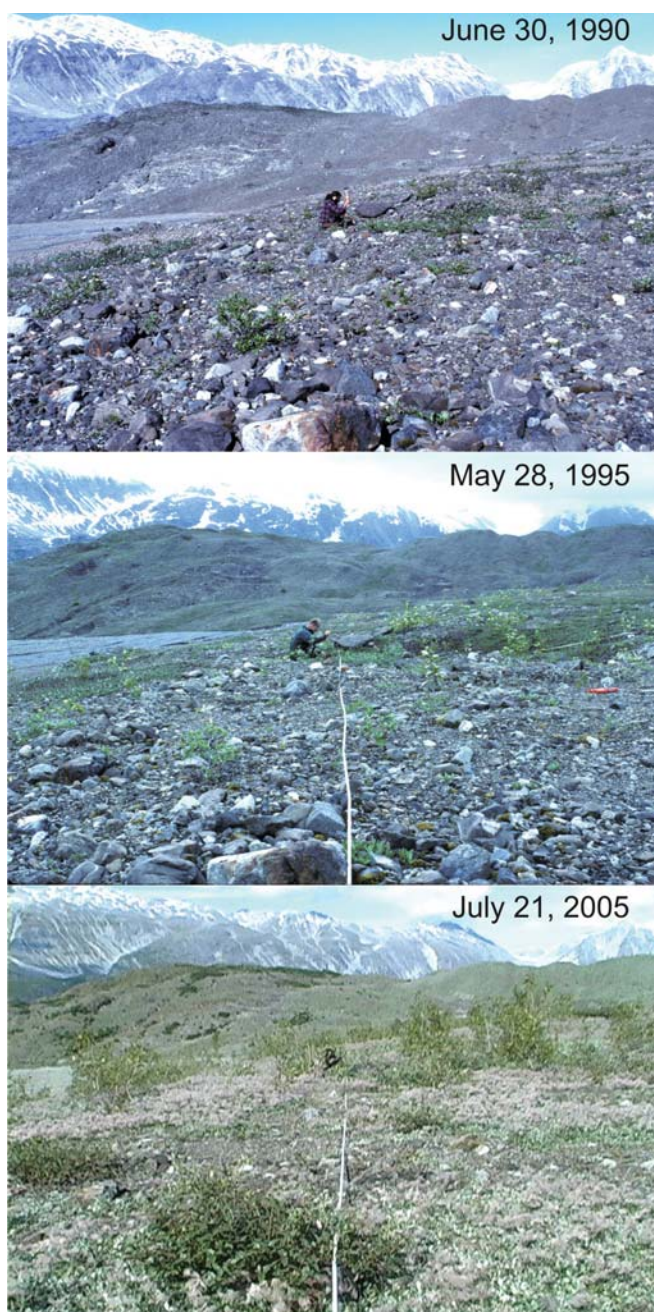

*Figure 4. A study plot near Muir Inlet, which became ice free in 1968. Between 1990 (top) and 2005 (bottom), colonizing plants spread across the glacial till surface, allowing biotic processes (e.g., the capture and accumulation of atmospheric carbon and nitrogen in plants and soil) to increase control over ecosystem structure and function, as physical processes (e.g., erosion, warming and dewatering of sediments, oxidation of minerals) became less important. Vegetation includes scattered shrubs (*Dryas* and willows) and cottonwood seedlings in 1990, and a continuous carpet of Dryas interrupted by scattered willow shrubs and cottonwood saplings in 2005. Seed sources of alder and spruce are distant from this site, limiting the early importance of those species. Photographs: Christopher L. Fastie.*

scutifer, Daphnia pulicaria) that can tolerate the damaging radiation (Olson et al. 1995, Williamson et al. 2001). Fish, if present, are limited to the euryhaline stickleback (*Gasterosteus aculeatus*) and Dolly Varden trout (*Salvelinus malma*), which immigrate from nearshore marine environments through streams and glacial drainages. Approximately half of all lakes and ponds remain fishless because of migration barriers (waterfalls) or lack of a stream connecting the lake to the sea.

Young streams without lakes initially support low macroinvertebrate diversity and abundance due to low channel stability and widely fluctuating flow regimes (Death and Winterbourn 1995). The unstable channels also typically provide poor habitat for spawning and rearing salmonid fish. The initial pioneers of these lakeless streams are Chironomidae (nonbiting midges), larvae of the genus *Diamesa,* whose long prolegs and strong claws enable them to cling to stones in fast-flowing, unstable channels (Milner and Petts 1994, Milner et al. 2000). Lakes play a major role in the biological development of downstream reaches of streams by buffering flow regimes and acting as a sediment trap to remove coarser material. In lake-influenced channels, pioneer chironomids are often abundant (> 4000 m^2) in the absence of competitors or predators, despite low water temperature (< 4°C). Lakes increase water temperature in these channels by providing a large surface area for absorption of solar radiation. Water temperature is a major determinant of the stream age at which macroinvertebrate taxa colonize the new stream channels and hence the overall successional sequence.

In the early stages of primary succession at Glacier Bay, riparian vegetation alongside streams may be minimal. Thus inputs of terrestrial organic material are low, and production from in-stream algae constitutes an important energy source, particularly where upstream lakes provide the channel stability to facilitate its growth. These algae occur in biofilms of microorganisms (bacteria, algae, fungi, protozoa), exoenzymes, and detritus particles emeshed in a gelatinous polysaccharide matrix on rock surfaces. Toward the end of this phase, willow catkin inputs from riparian vegetation are an important source of food (figure 2b) and facilitate colonization by certain chironomid and caddisfly larvae not found on streambed cobbles (Flory and Milner 1999). Certain caddisfly larvae are similarly dependent on terrestrial inputs and have been found only on alder roots protruding into the stream (Flory and Milner 1999).

Pacific salmon that stray from nearby streams typically colonize new streams and can establish significant populations within 20 years. In many small streams in southeastern Alaska, salmon carcasses increase biofilm and macroinvertebrate productivity by delivering marine-derived nutrients that support food webs (Wipfli et al. 1998, 1999, Gende et al. 2002, Naiman et al. 2002). These marine nutrients become incorporated into riparian vegetation as bears or birds drag salmon onto stream banks (Naiman et al. 2002). Surprisingly, this transfer of marine-derived nutrients into lotic food webs or riparian vegetation has not been observed to date in young

Glacier Bay streams such as Wolf Point Creek (< 50 years old and < 3 km in length; figure 1)—despite over 10,000 pink salmon spawning the previous summer (Milner et al. 2000)—perhaps because these streams typically lack habitat features important for carcass retention, such as pools and CWD.

Despite the lack of a large influx of marine-derived nutrients into streams flowing through young landscapes, the movement of pink salmon (*Oncorhynchus gorbuscha*) from the ocean to young streams is an important landscape process. The redds of pink salmon are typically 1.1 to 2.0 m^2 in area and 10 to 20 centimeters deep (Heard 1991), and where spawning densities are high, they substantially disturb the streambed, causing lower total macroinvertebrate abundance and diversity (Monaghan 2002, Moore et al. 2004). However, some macroinvertebrate taxa increase in relative abundance as disturbance by salmon creates streambed patches for colonization by fugitive species, which allows potentially poor competitors to persist in the community.

Community development is fundamentally different in the marine intertidal ecosystem than on land, because of the overriding control of physical variables such as summertime low water temperature, low salinity, high suspended-sediment concentration, and scouring of the shore by icebergs, all of which severely constrain the establishment of marine organisms. Consequently, intertidal communities close to tidewater glaciers (within 20 to 30 km) do not develop further, regardless of age. This can occur, for example, where the glaciers substantially slow or cease their retreat (e.g., Muir Glacier). However, when the physical environment changes, intertidal community development is very rapid, proceeding from uncolonized to fully colonized within a decade. Controlled reciprocal transplants of intertidal communities on boulders, as well as bare-boulder transplants, have clearly demonstrated that the physical environment, rather than time since deglaciation, controls intertidal community development in Glacier Bay (Sharman 1989). Colonized boulders transplanted 90 km from bay mouth to near-glacier sites showed massive mortality and decreased species richness, with virtually no recruitment. In contrast, communities transplanted from glacier face to bay mouth quickly (within three years) exhibited increased species richness and accelerated recruitment. Transplants of bare boulders into the intertidal zone at spaced intervals along the distance-from-glacier gradient were rapidly colonized and supported species richness levels similar to those of resident control boulders within three years.

This rapid colonization is a logical consequence of the life history traits of most intertidal organisms (dominated by benthic invertebrates and attached macroalgae), whose propagules are planktonic and rapidly disperse over long distances. Examples include barnacles, limpets, mussels, snails, sea stars, and algae such as *Fucus, Neorhodomela,* and *Acrosiphonia.* In addition, rapid generation times, early age of first reproduction, and short life span all contribute to this rapid development. The latter attributes also apply to freshwater organisms, with both groups differing substantially from most land plants.

In this early phase of development, ecosystem linkages indicate the strength of physical control, particularly with respect to the influence of proglacial lakes on the stream ecosystem and the overall role of sediment transport (figure 2a). Nevertheless, some biotic influences become apparent, including the role of terrestrial vegetation in stabilizing sediments, driving soil development, providing organic material to streams and lakes, and supporting terrestrial arthropods, which enhance aquatic food chains.

Increasing biotic control (50 to 150 years)

In this section we discuss processes that typically occur between 50 and 150 years after deglaciation (figures 2c, 3b). During the 20th century, hundreds of square kilometers of lowland terrain were deglaciated and colonized by dense shrub thickets along the shores of Muir Inlet, the northeastern arm of the Glacier Bay fjord. These shrub communities are dominated by N-fixing alder, with a component of emergent spruce. During a century of N fixation by alder, soil N accumulated from near 0 to 2600 kg per hectare (ha), 30% more than at older sites, where shrub thickets were short-lived, included less alder, and proceeded relatively quickly to spruce dominance (Crocker and Major 1955, Fastie 1995a). Century-old soils under alder have distinct O and A horizons and have accumulated 43 metric tons of organic C per ha. Although the fertile soils under alder thickets increase the growth of spruce seedlings (compared with younger, alder-free sites) and of spruce trees emerging above the shrubs (Chapin et al. 1994, Fastie 1995a), alder also competes with spruce. Germination and establishment of spruce are strongly inhibited by alder leaf litter, and spruce seedlings grow more slowly and accumulate less N and phosphorus (P) than when experimentally protected from alder root competition by trenches (Chapin et al. 1994). Also, the growth rate of spruce trees increases dramatically when they emerge above the alder, suggesting that shade and physical damage under the shrub canopy have a substantial inhibitory effect (Fastie 1995a). Thus inhibitory effects of alder reduce the population density of spruce and slow the emergence of spruce above the thicket, while facilitative effects enrich young spruce seedlings and increase the growth of spruce trees that survive to overtop the shrub thicket. The net effect is to produce a spruce forest vastly different in density, age and size structure, and tree growth rate than would result without long-term dominance by N-fixing shrub thickets (Fastie 1995b). Although alder thickets facilitate the growth of individual spruce trees, they have a strong inhibitory effect on the population growth of spruce.

The legacy of landscape position is illustrated by comparison of the developmental history of lakes embedded in catchments following differing successional pathways. During the first century and a half after deglaciation, there is a steady increase in lake water DOC and a gradual, though site-specific, rise in N availability (Engstrom et al. 2000). Both trends are correlated with the buildup of organic matter and N in terrestrial soils as plant biomass increases with

succession. However, N increases are much more pronounced in lakes with abundant N-fixing alder in their catchments during early stages of terrestrial succession than in lakes with catchments succeeding directly to spruce–hemlock forest (i.e., sites proximal to spruce and hemlock seed sources on the terminal moraine). These differences in lake trajectories are evident in the changing composition of fossil diatom assemblages in sediment cores from the lakes (Fritz et al. 2004). Nitrogen increases are marked by the rising abundance of benthic diatoms such as *Fragilaria brevistriata, Fragilaria construens,* and *Fragilaria pinnata.* Changes in lake productivity are also tied to N availability and hence to the pattern of terrestrial succession. Lakes with abundant alder in their catchments demonstrate more pronounced increases in diatom accumulation rates—a robust sediment-core proxy for whole-lake primary production (Engstrom and Fritz 2006).

Lake water pH and alkalinity (a measure of excess base cations) remain relatively unchanged over this same time frame (50 to 150 years), despite the rapid weathering of carbonates from catchment soils. Lakes eventually become more dilute (a decrease in major ions) and acidic as soil development proceeds, but during the first half-century of landscape maturation, a balance between the export of base cations through surface drainage and import through groundwater is sufficient to sustain alkalinity. Vascular plants (macrophytes) begin to colonize lakes during the first half-century of lake development. These early arrivals include *Potamogeton richardsonii, Potamogeton filiformis,* and *Chara* spp., taxa characteristic of high-alkalinity waters. Macrophyte beds increase the structural complexity of the aquatic environment and provide additional substrates for attached algae as well as habitat for cladocerans and other invertebrates.

The increased inputs of leaf litter and CWD to streams as plant succession proceeds strengthen the linkages between biotic processes occurring on land and in streams (figure 2c; Milner et al. 2000). For example, the chironomid *Polypedilum fallax,* a xylophagous (wood-eating) species associated with dead wood, is absent in streams younger than 100 years in age (Milner and Phillips 2005). As alder replaces willow in the riparian zone, willow catkin input decreases, thereby reducing the abundance or causing extinction of associated stream invertebrate taxa. On the other hand, alder supports higher terrestrial invertebrate mass per stem than later-successional spruce or hemlock (Allan et al. 2003) and therefore exports significantly more macroinvertebrates into adjacent streams (Piccolo and Wipfli 2002). These differences in the quantity, composition, and timing of terrestrial subsidies to streams influence food availability for drift-feeding salmonids (e.g., juvenile coho salmon).

The influence of lakes on stream systems is often lost during landscape evolution, when lakes become detached from streams as they change course or the lake becomes shallower. Indeed, there are very few older stream systems (150+ years) with flow-buffering lakes. The loss of a lake makes downstream reaches colder and less stable, and resets stream succession to an earlier stage in which some macroinvertebrate taxa are lost

and overall abundance and diversity decline. Channel instability also allows the return of some pioneer fugitive taxa (e.g., *Diamesa* chironomids and blackflies) as a result of reduced competition and predation. In time, the input of CWD from the forested floodplain stabilizes channels, even in the absence of lakes.

The loss of lakes in watershed development also weakens the linkage between streams and the ocean. Sockeye salmon (*Oncorhynchus nerka*) typically require a lake in a system to establish populations, because they usually spawn in streams above the lake or in margins of the lake. Some of the youngest systems containing lakes (< 50 years old) support sockeye salmon populations (e.g., Stonefly Creek and Gull Lake Creek in Wachusett Inlet), but other streams, such as Nunatak Creek and Vivid Stream (figure 1), have lost their sockeye populations as their lakes have become separated from the stream that provided a migratory corridor to the ocean.

The inertia of organic matter (more than 150 years)

In this section we discuss processes that typically occur 150 years or more after deglaciation (figures 2d, 3c). Regardless of its early-successional history, vegetation converges on some type of spruce forest two centuries after ice retreat. On 150-year-old surfaces, the broad crowns of fast-growing spruce trees begin to coalesce to form a continuous canopy over the alder thicket that dominated the site for a century. But this spruce forest differs dramatically from spruce forests on older surfaces where N-fixing alder did not form long-lasting thickets. Sites that became ice free 200 years earlier have only 60% of the ecosystem N pool, and 80% of the ecosystem C pool, of 150-year-old forests. Tree growth in the older forests has probably been N limited for many decades, and many of these forests have suffered lethal outbreaks of spruce bark beetles that preferentially mass-attack and kill slow-growing trees. Younger forests with ample alder-fixed N may avoid this standwide senescence, suggesting that initial landscape position, through its effect on successional trajectory, can substantially influence ecosystem function for centuries.

The chemistry of lakes continues to change for the next several centuries after deglaciation, and some of the more dramatic and ecologically important transformations do not begin until this time period. One of the more pervasive trends is a steady decline in lake water pH and the associated loss of alkalinity (Engstrom et al. 2000). These changes result from a reduction in the inflow of base cations and a parallel increase in DOC loading from the catchment. In part, the changes in runoff chemistry are a consequence of continued weathering of carbonates from upper soil horizons and the long-term buildup of soil organic matter. However, a reduction in groundwater inflow is, for most lakes, a more important process driving the alkalinity losses. Groundwater inflow declines because of long-term edaphic processes—in this case, the gradual formation of cemented soil hardpans and the eventual development of thick accumulations of peat (figure 3c). These changes gradually inhibit the infiltration of precipitation into the ground and increase surface runoff at the expense

of groundwater recharge. Because surface runoff coursing through peat or weathered soil horizons contains lower concentrations of base cations and higher concentrations of DOC than the groundwater it replaced, lakes receiving a greater proportion of these surface inputs gradually become more dilute and acidic.

In most lakes, alkalinity and pH declines do not begin until about 200 years after deglaciation and therefore are barely evident in lakes occupying the low-elevation forelands in Glacier Bay proper. However, on older surfaces—the early Neoglacial moraines (300 to 2000 years old) found along the outer coast of Glacier Bay National Park, and still older terrain (13,000 years old) in Icy Strait, beyond the mouth of Glacier Bay—dilute, DOC-stained lakes are the norm (Engstrom et al. 2000). Here, extensive peatlands are widespread, especially on gentle slopes at lower elevations, and lakes on these surfaces may have DOC levels exceeding 10 mg per L, a pH of 5 or less, and no carbonate buffering capacity (alkalinity = 0). What is more remarkable is that the underlying geology of these older surfaces is rich in carbonates, so that the lakes when originally created were similar in chemistry to the young, high-pH lakes forming near the retreating ice margins in Glacier Bay today.

These successional patterns have been inferred from a chronosequence of contemporary lakes (space-for-time substitution) as well as from the fossil diatom assemblages preserved in dated sediment cores from some of the older lakes. The diatoms, which are highly sensitive to pH, DOC, and alkalinity changes, leave a record that confirms the general pattern evident in the lake chronosequence but also indicates that lakes differ in their initial starting points and in the overall rate of change. Individual lake trajectories are largely explicable in terms of underlying differences in local geology and hydrology (particularly the relative importance of surface and groundwater inflows).

The biological changes that accompany the long-term trends in lake chemistry include a replacement of alkaliphilous, mid-successional diatom species by more acid-tolerant taxa, such as *Fragilaria virescens* v. *exigua, Cymbella gauemanii,* and *Aulacoseira* spp. (Fritz et al. 2004). The macrophyte community undergoes a similar transformation, as low-alkalinity taxa (*Nuphar, Menyanthes, Hippuris*) replace early-successional species, while zooplankton assemblages become more diverse, with large, predatory copepods (e.g., *Diaptomus kenai, Heterocope septentrionalis*) appearing in some of the older fishless lakes (Olson et al. 1995). Most of the diatoms are attached (benthic) species, although a limited planktonic community develops in some lakes over time. In-lake bioassay experiments indicate that DOC and nutrient concentrations, as well as alkalinity and pH, are important determinants of diatom community structure (Olson 1998). The influence of DOC is manifest through its effect on light regime (quality and quantity), whereas nutrient effects are primarily those due to N (not P) limitation. In some lakes, N concentrations begin to level off after about 150 years of deglaciation, which results in a decrease in overall ben-

thic production, as measured by accumulation of diatoms in sediment cores (Engstrom and Fritz 2006). The declines in lake water N and benthic production are a consequence of the reduced availability of soil N associated with primary terrestrial succession (replacement of N-fixing alder and sequestration of soil N in living and dead biomass). However, lake-specific nutrient and productivity trends depend highly on landscape position and on the variable importance of alder during the early stages of terrestrial succession.

Linkages between the terrestrial ecosystem and the stream ecosystem will be highest during this developmental period of more than 150 years (figure 2d). The CWD recruited from the forest proximal to the channel will accumulate in streams, especially where there is no upstream lake and the stream migrates across the floodplain. Coarse woody debris sufficiently large to span most of the channel increases stream habitat complexity and heterogeneity (Trotter 1990, Gurnell et al. 1995), provides cover and habitat for juvenile and spawning fish (Shirvell 1990), and supplies complex surfaces for the development of diverse invertebrate assemblages (O'Connor 1991). Accumulations of CWD are not observed in Glacier Bay streams until the streams are approximately 130 to 150 years old, when certain channel features, such as gravel bars, become stabilized by dead wood (Milner and Phillips 2005), which enhances the process of island formation and channel stability (Gurnell et al. 2005). Maximum levels of CWD are predicted to occur in nonlake streams after approximately 300 years, but at least an additional 100 years will be required in stable streams below lakes where dead wood entrainment is not enhanced by flooding, channel migration, and bank undercutting (Milner and Phillips 2005).

Coarse woody debris also increases the retention of salmon carcasses and leaf material and increases nutrient cycling rather than exporting the nutrients downstream. We have no information on the importance of hyporheic zones for retaining nutrients in fresh waters. Furthermore, wood is more stable than leaf litter and can support a greater density and diversity of biofilm and aquatic invertebrates (Hax and Golladay 1993). However, with improved retention, up to 30% of the N in juvenile salmon in older streams (e.g., in Berg Bay North stream > 150 years after deglaciation; figure 1) was found to be from marine sources (Milner et al. 2000). Hence these "gifts from the sea" (sensu Oswood et al. 2006) do not have a major influence on stream food webs until forest succession progresses and linkages with the terrestrial system increase (figure 2d).

The linkages in energy flow between stream and terrestrial environment are also strongest during this time period (figure 2d) and include aquatic adult insects, which provide food for riparian birds and for predaceous beetles and spiders on the floodplain (Nakano and Murakami 2001, Paetzold et al. 2005). There are also potential linkages between the marine environment and the terrestrial environment (via the fresh waters) through predators such as bears, which remove salmon from the stream, so that marine-derived N becomes incorporated into riparian vegetation (Gende et al. 2002, Helfield and Naiman 2006).

Marine intertidal communities become more diverse and exhibit greater trophic complexity as distance from the glacier increases and the physical environment moderates. Increasing distance ameliorates the environmental stresses associated with cold, low-salinity water; high levels of suspended sediment; and the scouring action on the shore by icebergs. However, whenever glaciers readvance, older communities are quickly reset to an earlier successional stage, just as observed in lakeless stream ecosystems. The intertidal zone also provides important rearing habitat for pink and chum fry before their ocean migration and is used by returning salmon before their migration upstream. Similarly, intertidal habitats are critically important to many transient terrestrial and marine vertebrates (during low and high tide, respectively) for purposes of foraging, shelter, and travel. Consequently, in combination with coastal stream mouths, the intertidal zone is the primary area where the physical transport of energy and materials between terrestrial and marine communities occurs.

Summary

Physical processes (temperature, substrate stability, and light and nutrient availability) initially dominated the dynamics of all four ecosystems at Glacier Bay after the glacial retreat, but the influence of biotic processes in each system has become increasingly important with time. The mechanisms responsible for this shift from physical to biotic control differ substantially and depend on the linkage strengths among ecosystems. Changes in the terrestrial system are dominated by vegetation effects on the physical and chemical environment that depend on the nature of propagule inputs from the surrounding landscape. Subsequent change in the terrestrial system on a large spatial scale is principally driven by biotic processes, although physical processes may alter successional trajectories on a local or patch scale (e.g., high water across a floodplain or storms causing windthrow). Biotic processes may also initiate patch-scale change through disease or pest infestations (e.g., spruce bark beetle).

Physical and chemical changes on land largely dictate the patterns of biotic development in lakes through changing inputs of sediment, organic C, N, and major ions. Similarly, close proximity to tidewater glaciers and turbid outwash streams severely limits community development in the intertidal ecosystem, regardless of substrate age. Biotic development proceeds only after glaciers retreat and no longer disturb a site with icebergs, sediments, and cold fresh water.

Streams exhibit the most complex development patterns, in part because of important linkages to biotic and physical processes in the other ecosystems. Stream community development depends on disturbances controlled by processes on land (sediment inputs and bank stabilization), in lakes (flow stabilization), and from the ocean (redd formation by salmon). The quantity of inputs to streams (sediments, leaf litter, and CWD) relates to the presence or absence of lakes to filter sediments, process DOC, or regulate flow (with consequences

for stream bank stability and recruitment of CWD). These terrestrial and lake effects on streams, in turn, determine the effectiveness with which streams retain salmon carcasses and therefore influence the transfer of marine-derived N to streams and riparian communities. However, the influence of lakes on stream channels may be only transitory, as siltation and changes in stream course allow few lake-influenced stream channels to persist past 50 years in Glacier Bay. Thus, change is not always unidirectional in the stream ecosystem, and benthic communities can be reset to an earlier successional state in which physical processes once again dominate stream development. Although the influence of biotic processes increases with stream ecosystem development, streams are unique among the four ecosystems in remaining more strongly dominated by physical processes.

All of the four ecosystems can revert to stronger physical control (e.g., via disturbance), but some are more prone to this than others. Soil development and biomass accumulation on land provide stable biotic structures and an inertia that is unequalled in stream, lake, or intertidal systems. This feature of terrestrial systems allows young plant communities to have important early influences on streams and lakes, and a continuing stabilizing influence throughout succession. On the other hand, terrestrial systems are uniquely prone to wildfire and wind. The low frequency of wildfire and destructive winds at Glacier Bay allows the terrestrial ecosystem to be unusually stable, and the strong linkages from the land to streams and lakes provide an important source of stability for those systems. Nonetheless, stream, lake, and intertidal systems are vulnerable to disturbances caused by moving water, to which most terrestrial systems are immune.

Many studies of succession and ecological development have considered ecosystems in isolation, but it is evident from our integration here at Glacier Bay that change in one ecosystem has a major influence on the nature and direction of change in other ecosystems. It is imperative that researchers and managers understand this science of change, at different spatial and temporal scales, so that we can adequately predict future states of ecological systems. The dynamics of change that we document here at Glacier Bay have important implications for managing the system with respect of anthropogenic change. Many of the most pronounced global changes result from land-cover changes due to land clearing and other disturbances (fire and flooding). These physical disturbances and subsequent biotic development have effects that propagate through the landscape and must be managed as an integrated system rather than individually within a single ecosystem. Restoration of ecosystems following anthropogenic disturbances is likely to increase in prominence during the next few decades, and our synthesis highlights the importance of understanding ecosystem linkages in managing landscape restoration.

Acknowledgments

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