The forgotten stage of forest succession: early-successional ecosystems on forest sites

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Early-successional forest ecosystems that develop after stand-replacing or partial disturbances are diverse in species, processes, and structure. Post-disturbance ecosystems are also often rich in biological legacies, including surviving organisms and organically derived structures, such as woody debris. These legacies and post-disturbance plant communities provide resources that attract and sustain high species diversity, including numerous early-successional obligates, such as certain woodpeckers and arthropods. Early succession is the only period when tree canopies do not dominate the forest site, and so this stage can be characterized by high productivity of plant species (including herbs and shrubs), complex food webs, large nutrient fluxes, and high structural and spatial complexity. Different disturbances contrast markedly in terms of biological legacies, and this will influence the resultant physical and biological conditions, thus affecting successional pathways. Management activities, such as post-disturbance logging and dense tree planting, can reduce the richness within and the duration of early-successional ecosystems. Where maintenance of biodiversity is an objective, the importance and value of these natural early-successional ecosystems are underappreciated.

Front Ecol Environ 2011; 9(2): 117–125, doi:10.1890/090157 (published online 2 Mar 2010)

Severe natural disturbances – such as wildfires, windstorms, and insect epidemics – are characteristic of many forest ecosystems and can produce a "stand-replacement" event, by killing all or most of the dominant trees therein (Figure 1). Typically, limited biomass is actually consumed or removed in such events, but many trees and other organisms experience mortality, leaving behind important biological legacies (structures inherited from the pre-disturbance ecosystem; Franklin *et al.* 2000), including standing dead trees and downed boles (tree trunks; Franklin *et al.* 2000). Such legacies provide diverse physical/biological properties and suitable microclimatic conditions for many species. Thereafter, species-diverse plant communities develop because substantial amounts of previously limited resources (light, moisture, and nutrients) become available. These emerging plant communities create additional habitat complexity and provide various energetic resources for terrestrial and aquatic organisms.

In a nutshell:

- Naturally occurring, early-successional ecosystems on forest sites have distinctive characteristics, including high species diversity, as well as complex food webs and ecosystem processes
- This high species diversity is made up of survivors, opportunists, and habitat specialists that require the distinctive conditions present there
- Organic structures, such as live and dead trees, create habitat for surviving and colonizing organisms on many types of recently disturbed sites
- Traditional forestry activities (eg clearcutting or post-disturbance logging) reduce the species richness and key ecological processes associated with early-successional ecosystems; other activities, such as tree planting, can limit the duration (eg by plantation establishment) of this important successional stage

The ecological importance of early-successional forest ecosystems (ESFEs) has received little attention, except as a transitional phase, before resumption of tree dominance. In forestry, this period is often called the "cohort re-establishment" or "stand initiation" stage, with attention obviously focused on tree regeneration and the re-establishment of closed forest canopies (Franklin *et al.* 2002). Ecological studies have focused primarily on plant-community development and the needs of selected animal (mostly game) species, and not on the diverse ecological roles of ESFEs.

Here, we highlight important features of ESFEs, including their role in sustaining ecosystem processes and biodiversity, so that they may be appropriately considered by resource managers and scientists, and included within management/research programs dedicated to maintaining these functions, particularly at larger spatiotemporal scales. Most published examples focus on sites in western North America, but ESFEs are important elsewhere (Angelstam 1998; DeGraaf *et al.* 2003). We also discuss how traditional forestry practices, such as clearcutting, tree planting, and post-disturbance logging, can affect early-successional communities.

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Figure 1. *Stand-replacement disturbance events in forests create large areas free of tree dominance and rich in physical and biological resources, including legacies of the pre-disturbance ecosystem.*

■ Early-successional ecosystems on forest sites

Initial conditions after stand-replacing forest disturbances vary generically, depending on the type of disturbance; this includes the types of physical and biological legacies available. For example, aboveground vegetation may be limited immediately after the disturbance, as in the case of severe wildfires or volcanic eruptions. Conversely, intact understory communities may persist where forests have been blown down by severe windstorms. Spatial heterogeneity in conditions is characteristic, given that disturbances vary greatly in the amount of damage they cause (Turner *et al.* 1998). For instance, severe wildfires frequently include substantial areas of unburned as well as low to medium levels of mortality, creating variability in shade, litterfall, soil moisture, seed distribution, and other factors.

We define ESFEs as those ecosystems that occupy potentially forested sites in time and space between a stand-replacement disturbance and re-establishment of a closed forest canopy. These ecosystems undergo compositional and structural changes (succession) during their occupancy of a site. Changes begin immediately post-disturbance, as a result of the activities of surviving organisms (eg plants, animals, and fungi), including plant growth and seed production. Developmental processes are enriched by colonization of flora and fauna from outside the disturbed area. Successional change is often characterized by progressive dominance of annual and perennial herbs, shrubs, and trees, although all of these species are typically represented throughout the entire sequence of forest stand development (or sere; Halpern 1988).

The ESFE developmental stage ends with re-establishment of tree cover that is sufficiently dense to suppress and often eliminate many smaller shade-intolerant plants (Franklin *et al.* 2002). Consequently, the duration of ESFEs varies inversely with rapidity of tree regeneration and growth, which, in turn, depend on such variables as tree propagule availability, conditions affecting seedling or sprout establishment, and site productivity. ESFE longevity after natural disturbances is therefore highly variable.

Development of a closed forest canopy may require a century or more in areas with limited seed sources, harsh environmental conditions, severe shrub competition (in some instances), or combinations thereof (Hemstrom and Franklin 1982). For example, tree canopy closure after wildfire in the Douglas fir region of western North America often requires several decades (Poage *et al.* 2009), but can occur much more rapidly when canopy seedbanks are abundant (eg Larson and Franklin 2005). Closed forest canopies may develop quickly in forests dominated by trees with strong sprouting ability (eg many angiosperms) or when windstorms "release" understories of shade-tolerant tree seedling banks by removing all or most of the overstory (Foster *et al.* 1997).

■ Attributes of early-successional ecosystems

After severe disturbances, forest sites are characterized by open, non-tree-dominated environments, but have high levels of structural complexity and spatial heterogeneity and retain legacy materials.

Environmental conditions

Removal of the overstory forest canopy during disturbances dramatically alters the site's microclimate, including light regimes. These changes lead to increased exposure to sunlight, more extreme temperatures (ground and air), higher wind velocities, and lower levels of relative humidity and moisture in litter and surface soil. Shifts in these environmental metrics favor some species, while creating suboptimal or intolerable conditions for others. For example, post-disturbance plant community composition, cover, and physiognomy are altered as shade-tolerant understory herbs are largely displaced by shade-intolerant and drought-tolerant species. New substrates deposited by floods or volcanic eruptions may lack nutrients, provide additional water-holding capacity, or have high albedo, all of which favor shifts in plant communities.

Survivors

Organisms (in a variety of forms) that survive severe disturbances are extremely important for repopulating and restoring ecosystem functions in the post-disturbance landscape. Even in severely disturbed areas, organisms may survive as individuals (mature or immature) or as reproductive structures (eg spores, seeds, rootstocks, and eggs), which become in situ propagule sources. For example, after the 1980 volcanic eruption of Mount St Helens (Washington State), most pre-eruption flora and many fauna (especially aquatic and burrowing terrestrial species) survived within the blast zone through several different mechanisms (Dale *et al*. 2005).

Surviving organisms are also often vital for the prompt re-establishment of important ecosystem functions, such as conservation of nutrients and stabilization of substrates. For instance, the important role of resprouting vegetation in curbing massive losses of nitrogen was demonstrated by experimentally clearcutting and applying herbicides in a watershed at Hubbard Brook Experimental Forest (Bormann and Likens 1979).

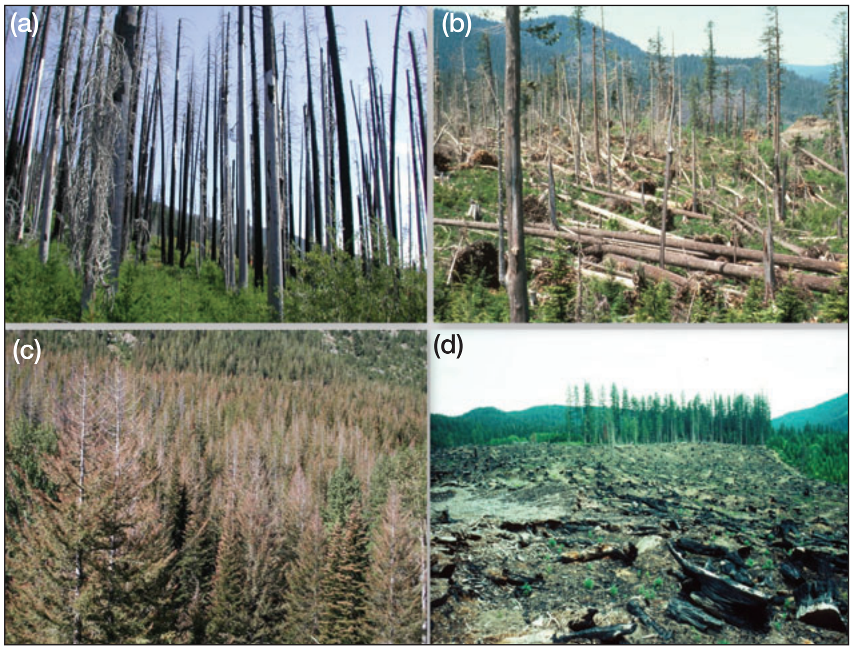

Figure 2. *Different types of disturbances produce different types of biological legacies, including living organisms and structures: (a) standing dead trees (snags) are dominant structural legacies after severe wildfires; (b) downed tree trunks and nearly intact understory communities are characteristic legacies after major windstorms; (c) standing dead trees are also dominant structural legacies after heavy insect infestations; and (d) clearcuts typically eliminate most aboveground structural legacies. Values for each metric are shown in Table 1 and are described in detail in the text.*

Structural complexity

The structural complexity of ESFEs depends initially on legacies, the general nature of which varies with the type of disturbance (Table 1; Figure 2); for example, snags and shrubs originating from belowground perennating (ie resprouting) parts or seeds are dominant legacies after wildfires, whereas downed boles and largely intact understories are typical post-disturbance characteristics of windstorms.

Woody legacies, such as snags and downed boles, play numerous roles in structuring and facilitating the development of the recovering ecosystem – providing habitat for survivors and colonists, moderating the physical environment, enriching aquatic systems in the disturbed area (Jones and Daniels 2008), and providing long-term sources of energy and nutrients (Harmon *et al*. 1986). Although subject to decomposition, these legacies can persist for many decades and sometimes even centuries.

Table 1. Different types of intense disturbances generate different types of biological legacies

	Disturbance				
Biological legacies	*Wildfire*	*Wind*	*Insect*	*Volcano*	*Clearcut*
Live trees	Infrequent	Variable	Variable (depends on stand composition)	Infrequent – confined to margins	Infrequent or absent
Snags	Abundant	Variable	Abundant	Abundant (spatially variable)	Infrequent or absent
Downed woody debris	Variable, but typically abundant	Abundant	Variable, but eventually abundant	Abundant (spatially variable)	Infrequent
Undisturbed understory	Infrequent	Abundant	Abundant	Infrequent – confined to disturbance margins	Infrequent
Spatial heterogeneity of recovery	High	Variable	High	High	Variable – usually low
Time in early-successional condition	Variable	Variable	Long	Variable – usually long	Variable – usually short

Figure 3. *Plant communities with well-developed shrub and perennial herb species are characteristic of early-successional communities on forest sites and provide diverse food resources. Twenty-five years after the Mount St Helens eruption in 1980, this community, which was within the blast zone, includes well-developed shrubs (eg* Sorbus *and* Vaccinium *spp), trees, and perennial herbs (eg* Epilobium angustifolium*).*

Structural complexity is further enhanced by the establishment and development of a variety of plant species, which often include perennial herbs and shrubs characteristic of open environments, as well as individual trees (Figure 3). The diversity of plant morphologies (maximum height, crown width, etc) increases structural richness, so that this associated flora contributes to both horizontal and vertical heterogeneity.

Spatial heterogeneity

Spatial heterogeneity is evident in early-successional ecosystems and has multiple causes: (1) natural variability in the geophysical template (topography and lithology) of the affected landscape; (2) variability in conditions in the pre-disturbance forest ecosystem; (3) variability in the intensity of the disturbance event; and (4) variability in rates and patterns of subsequent developmental processes in the ESFE. The first two sources relate to existing geophysical and biological patterns within the disturbed area. Land formations and patterns of geomorphic processes are certainly key geophysical elements (Swanson *et al.* 1988). The presence of surface water, such as streams and ponds, can be particularly influential in facilitating survival and re-establishment of biota.

Natural disturbances create heterogeneous environments at multiple spatial scales (Heinselmann 1973), because disturbances do not cause damage uniformly. Disturbances such as wildfires and windstorms are variable in intensity (eg "spotting", or initiation of new flame fronts by wind-thrown firebrands, during fire events). Alternatively, geographic variation in environmental conditions and topography (Swanson *et al.* 1988) influences the intensity of the disturbance and results in heterogeneity at multiple scales. Variability in the structure and composition of the pre-disturbance forest also creates spatial and temporal variability (Wardell-Johnson and Horowitz 1996). Some of these patterns may be transient, such as residual snowbanks protecting tree regeneration after the aforementioned Mount St Helens eruption (Dale *et al.* 2005).

Post-disturbance developmental processes also lead to spatial heterogeneity. For example, varying distances to sources of tree seed result in different rates and densities of tree re-establishment (Turner *et al.* 1998). Structural legacies can greatly influence the rates at which wind- or waterborne organic (including propagules) and inorganic materials are deposited. Finally, animal activity can strongly influence patterns of revegetation, as illustrated by the multiple effects that gophers (*Thomomys* spp) can have on post-disturbance landscapes (Crisafulli *et al.* 2005b) or the way ungulate browsing may impede tree regeneration (Hessl and Graumlich 2002).

Biological diversity

ESFEs in temperate forest seres show great diversity in the abundance of plant and animal species (Fontaine *et al.* 2009). Species composition may consist of a mix of forest survivors, opportunists, or ruderals (plants that grow on disturbed or poor-quality lands), and habitat specialists that co-exist in the resource-rich ESFE environment (Figure 3). Most forest understory flora can survive disturbances as established plants, perennating rootstocks, or seeds. In one study, in western North America, over 95% of understory species survived the combined disturbance of logging and burning of an old-growth Douglas-fir–western hemlock stand (Halpern 1988). Some important early-successional species (eg *Rubus* spp [blackberry; raspberry], *Ribes* spp [gooseberry], and *Ceanothus* spp [buckbrush]) may persist as long-lived seedbanks.

Opportunistic herbaceous species are often conspicuous dominants early in the development of ESFEs (Figure 4). Many of these weedy species (particularly annuals) decline quickly, although other opportunists will persist as part of the plant community until overtopped by slower growing shrubs or trees. Consequently, diverse plant communities of herbs, shrubs, and young trees emerge in ESFEs; this, combined with the structural legacies from the pre-disturbance ecosystem, often results in high levels of structural richness (Figure 3).

Many animals, including habitat specialists and species typically absent from the eventual tree-dominated communities, thrive under the conditions found in ESFEs. For some species, this is the only successional stage that can provide suitable foraging or nesting habitat. As an example, many butterflies and moths (Lepidoptera) found in forested regions depend on the high diversity and quality of plant forage in ESFEs (eg Miller and Hammond 2007), whereas jewel beetles (Coleoptera: Buprestideae) depend on abundant coarse woody debris. Also, a number of ground-dwelling beetle species occur as habitat specialists in early-successional communities (Heyborne *et al.* 2003).

Figure 4. *Early-successional communities are often dominated by annual herbaceous species for the first few years after disturbance; these are quickly displaced by perennial herbaceous species and shrubs.*

Many vertebrates also respond positively to ESFEs, which may provide the only suitable habitat at a regional scale for some species. Ectothermic animals, such as reptiles (eg Rittenhouse *et al.* 2007), generally respond favorably to sunnier and drier conditions, colonizing early-successional habitat or increasing in abundance if present as survivors. Many amphibians also thrive in ESFEs, provided resources such as water bodies and key structures (eg logs) are available. The diversity and abundance of amphibians in the area affected by the 1980 Mount St Helens eruption is illustrative (Crisafulli *et al.* 2005a); eleven of 15 amphibian species survived the event, and some (eg western toad, *Bufo boreas*) have since had exceptional breeding success.

The broad array of birds using the abundant and varied food sources (eg fruits, nectar, herbivorous insects) and nesting habitat in ESFEs includes many raptors and neotropical migrants, often making bird diversity highest during the ESFE stage of succession (Klaus *et al.* 2010). Some species are habitat specialists that directly utilize the legacy of recently killed trees; for instance, black-backed woodpeckers (*Picoides arcticus*) are almost completely restricted to early post-fire conditions (Hutto 2008). Mountain bluebirds (*Sialia currucoides*) and several other woodpecker species also favor structurally rich, early-successional habitats (Figure 5). Observed population declines of many avian species in eastern North America – which, in some cases, have proceeded to a point of conservation concern – are linked to conversion of early-successional habitat to closed forest (Litvaitis 1993).

Small mammal communities in ESFEs typically show high levels of diversity as well, including some obvious habitat specialists. The eastern chestnut mouse (*Pseudomys gracilicaudatus*), for example, inhabits early-successional environments in coastal eastern Australia for 2–5 years after a wildfire, and then declines dramatically until these environments are burned again (Fox 1990). Populations of mesopredators (medium-sized predators, such as raccoons [*Procyon lotor*] and fox species) benefit from the abundance of small vertebrate prey items characteristic of ESFEs. Likewise, some species of large mammals are well known to favor ESFEs (Nyberg and Janz 1990). Utilizing the diverse and luxuriant forage characteristically present in these ecosystems, ungulates, such as members of the Cervidae, in turn serve to benefit large predators (eg wolves [*Canis lupus*]) as well as scavengers, making ESFEs important elements within those species' typically extensive home ranges. Omnivores, such as bears (*Ursus* spp), also rely on the diversity of food sources often present in ESFEs.

■ Food web diversity

ESFEs are exceptional in the diversity and complexity of food webs they support. Simply stated, a diverse plant community produces many food sources. Food resources for herbivores (grasses, shrubs, forbs) – as well as nectar, seeds, and shrub-borne fruit (eg produced by *Rubus* and *Vaccinium* spp [huckleberry]) – can reach high levels before site dominance by trees. In the temperate Northern Hemisphere, biologically important berry production is maximized in slowly reforesting ESFEs. Resource production in early-successional patches may even augment the richness of adjacent undisturbed forests, as in the case of fluxes of key prey species (Sakai and Noon 1997).

Aquatic biologists have, perhaps, best appreciated the greater complexity of food chains in early-successional versus closed forest environments (Bisson *et al.* 2003). In established forest stands, trees strongly dominate the physical and biological conditions in nearby small streams by controlling light and temperature, stabilizing channels, providing woody debris, and, importantly, offering allochthonous inputs (organic matter originating outside the aquatic ecosystem) – the primary energy and nutrient source for such ecosystems (Vannote *et al.* 1980).

Stand-replacement disturbances remove forest constraints on conditions and processes, and shift streams to an early-

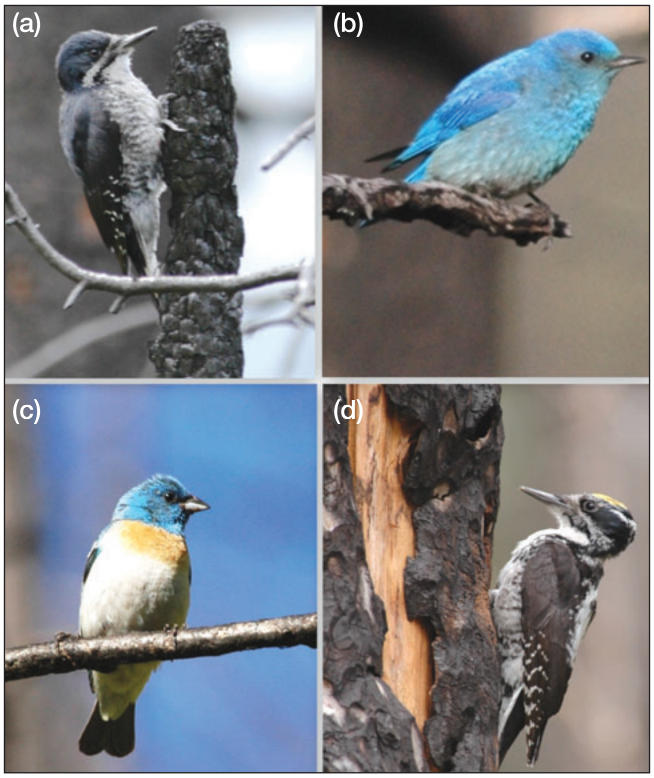

Figure 5. *Bird diversity is typically high in early-successional communities on forest sites and includes many habitat specialists: (a) black-backed woodpeckers (*Picoides arcticus*) are almost entirely restricted to early post-fire habitat; (b) mountain bluebirds (*Sialia currucoides*) favor early-successional ecosystems; (c) lazuli buntings (*Passerina amoena*) and (d) three-toed woodpeckers (*Picoides tridactylus*) have similar requirements.*

successional context (Minshall 2003; Figure 6). This greatly diversifies the types and timing of allochthonous inputs, as well as increases primary productivity. Allochthonous inputs are shifted from primarily tree-derived litter (coniferous-based in many systems) to material from a range of flowering herbs, shrubs, and trees, as well as from conifers. Consequently, litter inputs are highly variable in quality (eg decomposability) and delivery time, as compared with litterfall contributed primarily by evergreen conifer species. Also, inputs to post-disturbance streams often include material with a high nitrogen content, such as litter from the early-successional genera *Alnus* and *Ceanothus* (Hibbs *et al.* 1994).

Greater algal production may increase the diversity and abundance of aquatic invertebrate populations, which, in turn, become prey for fish and other organisms. However, increases in sediment production associated with disturbances can negate some benefits to aquatic processes and organisms (Gregory *et al.* 1987).

■ Processes in ESFEs

Ecosystem processes in ESFEs can be more diverse than those in closed forest systems, where the primary productivity of trees is dominant and organic matter is processed primarily through detrital food webs. Development of more diverse, and perhaps more "balanced", trophic pathways is possible when a disturbance opens a previously closed forest canopy. The contrast is probably greatest in forests dominated by a single tree type, such as evergreen conifers, as opposed to more diverse forests, such as mixed evergreen associations.

Recharging nutrient pools

ESFEs provide major opportunities for recharge of nutrient pools, such as additions to the nitrogen pool by leguminous (eg *Lupinus*) and some non-leguminous early-successional (eg *Alnus* and *Ceanothus*) plant species. These genera are commonly absent from late-successional forests, but are well represented in ESFEs. Nitrogenous additions from these sources are particularly important where the disturbance – eg a wildfire – has volatilized a substantial amount of the existing nitrogen pool.

Mineralization rates of organic material are typically accelerated (sometimes profoundly) after disturbances, as a result of warmer growing season temperatures. Diversified litter inputs in ESFEs, including a greater proportion of easily decomposed litter from herbs and deciduous shrubs, also result in more rapid mineralization. Finally, successional changes in the fungal and microbial communities can also hasten decomposition processes. As noted, these changes will be most profound in forest ecosystems dominated by a single species, including evergreen conifers or hard-leaved, evergreen hardwoods (such as the ash-type eucalypt forests of southeastern Australia).

In aquatic ecosystems that experience fire in adjacent forests, greater post-disturbance light and nutrient availability enhance primary productivity within the water body, causing shifts in food webs from the level of primary producers up through high-level consumers, such as fish (Spencer *et al.* 2003).

Modifying hydrologic and geomorphic regimes

Hydrologic regimes associated with ESFEs contrast greatly with those characterizing closed forest cover. For example, transpiration and interception are dramatically reduced and recover only gradually as forest canopies redevelop. Increases in normally low summer flows and annual water yields may occur immediately after a disturbance, as compared with levels in the dense young forests that may subsequently develop (Jones and Post 2004). The opposite may be true in systems where condensation of cloud or fog on tree crowns is an important component of the hydrologic cycle. ESFEs may also contribute to increased discharge peak runoff flows in hydrologic events of smaller magnitude (Harr 1986), but appear to have little effect on the magnitude of peak flows during large runoff events (Grant *et al.* 2008). From an ecological perspective, this may have a positive outcome, however, because floods restructure and rejuvenate many riparian communities (Gregory *et al.* 1991).

Rates and patterns of geomorphic processes, such as erosion and nutrient leaching losses, are also different between ESFEs and later successional stages. Tree death results in a loss of root strength that is critical for stabilizing soils and deeper rock layers on mountain slopes (Perry *et al.* 2008). Erosion and landslides may occur at higher rates in ESFEs, contributing to the variability of sediment budgets in watersheds (Reeves *et al.* 1995) and creating long-lasting substrates for ruderals. While enhancing erosion processes, ESFEs also provide materials and processes that counteract this effect, such as woody debris, which retain sediments and organic materials, and surviving vegetation, which stabilizes slopes and nutrient stores (eg Bormann and Likens 1979).

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Figure 6. *Streams within early-successional forest ecosystems contrast with forest-dominated reaches in many ecosystem attributes, including physical parameters (temperature and insolation), structure, plant and animal composition, and ecosystem processes, such as primary productivity.*

■ Land management implications

Incorporating ESFE attributes into forest policy and management is highly desirable, given the numerous advantages provided by these ecosystems. Many species and ecological processes are strongly favored by conditions that develop after stand-replacement disturbances. Rapid, artificially accelerated "recovery" of disturbed forest areas (eg via dense planting) to closed forest conditions has serious implications for many species. Clearly the term "recovery" has a different meaning for such early-successional specialists or obligates.

To fulfill their full ecological potential, ESFEs require their full complement of biological legacies (eg dead trees and logs) and sufficient time for early-successional vegetation to mature. Where land managers are interested in conservation of the biota and maintenance of ecological processes associated with such communities, forest policy and practices need to support the maintenance of structurally rich ESFEs in managed landscapes. Natural disturbance events will provide major opportunities for these ecosystems, and managers can build on those opportunities by avoiding actions that (1) eliminate biological legacies, (2) shorten the duration of the ESFEs, and (3) interfere with stand-development processes. Such activities include intensive post-disturbance logging, aggressive reforestation, and elimination of native plants with herbicides.

In particular, post-disturbance logging removes key structural legacies, and damages recolonizing vegetation, soils, and aquatic elements of disturbed areas (Foster and Orwig 2006; Lindenmayer *et al.* 2008). Where socioeconomic considerations necessitate post-disturbance logging, variable retention harvesting (retention of snags, logs, live trees, and other structures through harvest) can maintain structural complexity in logged areas (Eklund *et al.* 2009).

Prompt, dense reforestation can have negative consequences for biodiversity and processes associated with ESFEs, by dramatically shortening their duration. Such efforts reduce spatial and compositional variability characteristic of natural tree-regeneration processes, promote structural uniformity, and initiate intense competitive processes that eliminate elements of biodiversity that might otherwise persist. Artificial reforestation can also reduce genetic diversity by favoring dominance by fewer tree species/genotypes, and may make the system more prone to subsequent, high-severity disturbances (Thompson *et al.* 2007). The elimination of shrubs and broad-leaved trees through herbicide application can alter synergistic relationships, such as the belowground mycorrhizal processes provided by certain shrub species (eg *Arctostaphylos* spp).

Naturally regenerated ESFEs are likely to be better adapted to the present-day climate and may be more adaptable to future climate change. The diverse genotypes in naturally regenerated ESFEs are likely to provide greater resilience to environmental stresses than nursery-grown, planted trees of the same species. Given that climate change is also resulting in altered behavior of pests and pathogens (Dale *et al.* 2001), encouraging greater tree species diversity may also increase ecosystem resilience.

Clearcutting has been proposed as a technique to create ESFEs, but this can provide only highly abridged and simplified ESFE conditions. First, traditional clearcuts leave few biological legacies (eg Lindenmayer and McCarthy 2002), limiting habitat and biodiversity potential. Second, clearcuts are often quickly and densely reforested, and often involve the use of herbicides to limit competition with desired tree species. Clearcuts can provide some early-successional functionality (eg serving as nurseries or post-breeding habitat for many bird species in the southern US; Faaborg 2002), but this service is often truncated by prompt reforestation.

Management plans should provide for the maintenance of areas of naturally developing ESFEs as part of a diverse landscape. This should be in reasonable proportion to *historical* occurrences of different successional stages, as based on region-specific historical ecology. Major disturbance events provide managers with opportunities to incorporate a greater diversity of species and processes in forest landscapes and to enhance landscape heterogeneity. Some aspects of ESFEs can be incorporated into areas managed for production forestry as well, such as through variable retention harvest methods, the incorporation of natural tree regeneration, and extending the duration of herb/shrub communities in some portions of a stand by deliberately maintaining low tree stocking levels.

Finally, we suggest that adjustments in language are needed. Ecologists and managers often refer to "recovery" when discussing post-disturbance ecosystems, inferring that early seral conditions are undesirable and need to be restored to closed canopy conditions as quickly as possible. Emphasizing recovery as the management goal fails to acknowledge the essential ecological roles played by early-successional ecosystems on forest sites. It should also be considered that climate change and other factors may not permit "recovery" to pre-disturbance conditions.

Conclusions

Twentieth-century forest management objectives were centered on wood production and, later, on conservation and development of late-successional forests. Rapid regeneration of dense timber stands was frequently seen as a way to address both of these divergent objectives. Recognizing the ecological value of early-successional ecosystems on forest sites extends the ecological concerns associated with old growth to another "rich" period in a forest sere. This represents an important development in the evolution of holistic management of forest ecosystems, whereby large landscapes are managed for diverse seral stages.

ESFEs provide a distinctive mix of physical, chemical, and biological conditions, are diverse in species and processes, and are poorly represented and undervalued in traditional forest management. Forest policy and practice must give serious attention to sustaining substantial areas of ESFEs and their biological legacies. Similarly, scientists need to initiate research on the structure, composition, and function of ESFEs in different regions and under different disturbance regimes, as well as on the historical extent of these systems, to serve as a reference for conservation planning.

Acknowledgements

We are grateful to KN Johnson for insightful comments. JFF, CMC, MES, and FJS thank the US Forest Service, the Pacific Northwest Research Station, the Wind River Canopy Crane, and the National Science Foundation for support of long-term ecological research at the HJ Andrews and Wind River Experimental Forests and at Mount St Helens. DAD acknowledges the Wilburforce Foundation for support. RLH acknowledges the Joint Fire Science Program (04-2-1-106) for support. We thank J Halofsky for Figure 6.

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