

<https://helda.helsinki.fi>

Helda

Hemiboreal forest: natural disturbances and the importance of ecosystem legacies to management

Jõgiste, Kalev

Wiley Blackwell

2017

Jõgiste, K, Korjus, H, Stanturf, J A, Frelich, L E, Baders, E, Donis, J, Jansons, A, Kangur, A, Köster, K, Laarmann, D, Maaten, T, Marozas, V, Metslaid, M, Nigul, K, Polyachenko, O, Randveer, T & Vodde, F 2017, 'Hemiboreal forest: natural disturbances and the importance of ecosystem legacies to management', *Ecosphere*, vol. 8, no. 2, pp. e01706-n/a. <https://doi.org/10.1002/ecs2.1706>

<http://hdl.handle.net/10138/178729>

10.1002/ecs2.1706

cc_by

publishedVersion

Downloaded from Helda, University of Helsinki institutional repository.

This is an electronic reprint of the original article.

This reprint may differ from the original in pagination and typographic detail.

Please cite the original version.

Hemiboreal forest: natural disturbances and the importance of ecosystem legacies to management

KALEV JÖGISTE,^{1,2,†} HENN KORJUS,¹ JOHN A. STANTURF,³ LEE E. FRELICH,² ENDIJS BADERS,⁴
 JANIS DONIS,⁴ ARIS JANSONS,⁴ AHTO KANGUR,¹ KAJAR KÖSTER,^{1,5} DIANA LAARMANN,¹
 TIIT MAATEN,¹ VITAS MAROZAS,⁶ MAREK METSLAID,¹ KRISTI NIGUL,¹ OLGA POLYACHENKO,¹
 TIIT RANDVEER,¹ AND FLOORTJE VODDE¹

¹*Institute of Forestry and Rural Engineering, Estonian University of Life Sciences, Kreutzwaldi 5, 51014 Tartu, Estonia*

²*Department of Forest Resources, University of Minnesota, 115 Green Hall, 1530 Cleveland Avenue North, St Paul, Minnesota 55108 USA*

³*Center for Forest Disturbance Science, USDA Forest Service, 320 Green Street, Athens, Georgia 30602 USA*

⁴*Latvian State Forest Research Institute "Silava", Rīgas 111, 2169 Salaspils, Latvia*

⁵*Department of Forest Sciences, University of Helsinki, Latokartanonkaari 7, 00014 Helsinki, Finland*

⁶*Faculty of Forestry and Ecology, Institute of Environment and Ecology, Aleksandras Stulginskis University, Studentu 11, Akademija, 53361 Kaunas District, Lithuania*

Citation: Jõgiste, K., H. Korjus, J. A. Stanturf, L. E. Frelich, E. Baders, J. Donis, A. Jansons, A. Kangur, K. Köster, D. Laarmann, T. Maaten, V. Marozas, M. Metslaid, K. Nigul, O. Polyachenko, T. Randveer, and F. Vodde. 2017. Hemiboreal forest: natural disturbances and the importance of ecosystem legacies to management. *Ecosphere* 8(2): e01706. 10.1002/ecs2.1706

Abstract. The condition of forest ecosystems depends on the temporal and spatial pattern of management interventions and natural disturbances. Remnants of previous conditions persisting after disturbances, or ecosystem legacies, collectively comprise ecosystem memory. Ecosystem memory in turn contributes to resilience and possibilities of ecosystem reorganization following further disturbance. Understanding the role of disturbance and legacies is a prerequisite for maintaining resilience in the face of global change. Several legacy concepts discussed in the peer-reviewed literature, including disturbance, biological, soil, land-use, and silvicultural legacies, overlap in complex ways. Here, we review these established legacy concepts and propose that the new terms “material legacy” (individuals or matter, e.g., survivors, coarse woody debris, nutrients left after disturbance) and “information legacy” (adaptations to historical disturbance regimes) cut across these previous concepts and lead to a new classification of legacies. This includes six categories: material legacies with above- and belowground, and biotic and abiotic categories, and information legacies with above- and belowground categories. These six legacies are influenced by differential patterns of editing and conditioning by “legacy syndromes” that result from natural or human-manipulated disturbance regimes that can be arranged along a gradient of naturalness. This scheme is applied to a case study of hemiboreal forests in the Baltic States of Estonia, Latvia, and Lithuania, where natural disturbance, traditional clearcut silviculture, and afforestation of abandoned agricultural lands constitute the three main legacy syndromes. These legacy syndromes in turn influence forest response to management actions and constrain resilience, leading to a mosaic of natural, manipulated, and artificial (novel) ecosystems across the landscape, depending on how the legacies in each syndrome affect ecological memory.

Key words: ecosystem legacies; ecosystem memory; information legacy; legacy syndrome; material legacy; natural disturbances.

Received 29 September 2016; revised 13 January 2017; accepted 13 January 2017. Corresponding Editor: Debra P. C. Peters.

Copyright: © 2017 Jõgiste et al. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** kalev.jogiste@emu.ee

INTRODUCTION

New paradigms of forest resource management that seek to meet a broader range of social objectives than timber supply have been proposed under various names, progressing in time from multiple-use (Bowes and Kruttila 1989) to ecosystem management (Christensen et al. 1996), from the regulated forest to near-to-nature forestry (Peterken 1999). To varying degrees, these paradigms have shifted from emphasizing wood supply to addressing needs imposed by changes in the environment and expectations from human society. Emulating natural disturbance regimes that result in more diverse forest structure and composition (Attiwill 1994, Suffling and Perera 2004) provides the main conceptual framework for alternative management approaches including continuous cover forestry (Pommerening and Murphy 2004), biodiversity restoration (Stanturf et al. 2014*a, b*), and close-to-nature forestry (Kangur et al. 2005, O'Hara 2016). This has been mirrored in ecology with the relatively recent recognition of the role that disturbances play in structuring ecosystems (White and Pickett 1985, White and Jentsch 2001, Franklin et al. 2002).

These new management paradigms share at least one defining characteristic: They place great value on maintaining or restoring “natural” conditions, including natural disturbance regimes. They differ in their approaches to the challenge of ecological complexity (Kuuluvainen 2009, Puettmann et al. 2009) and in defining natural conditions (Bradshaw 2005, Putz and Redford 2010, Chazdon et al. 2016). Nevertheless, all recognize to some degree the dynamics of ecosystems and responses to disturbances (Bradshaw and Sykes 2014) including the significance of persistent effects of previous disturbances. These effects have been described as “legacies” in an ecological context around the turn of the century (e.g., White and Harrod 1997, Franklin et al. 2000). Since then, legacies have been defined differently and named accordingly, depending upon the specific focus of analysis. Thus, there is considerable overlap among definitions of what have been termed disturbance, biological, soil, land-use, and silvicultural legacies.

Our objectives in this paper were to examine the several definitions of legacies and propose a classification of ecosystem legacies that subsumes

the other definitions and minimizes overlap. We recognize two types of legacies—material and information—that were recently proposed by Johnstone et al. (2016); material legacies are remnant individuals or matter that persists after a disturbance event, while information legacies are adaptations to historical (natural) disturbance regimes described by presence, frequency, and distribution of species traits that constrain ecosystem responses to an individual, contemporary disturbance event. As discussed in greater detail below, we propose that these concepts of information and material legacies apply more broadly than the natural disturbance context in Johnstone et al. (2016). In this paper, material and information legacies are affected by three levels of disturbances: natural disturbance, land use, and silviculture. Each edits the material legacy in a different fashion, and filters the information legacy via ecological variability and contingency conditions of individual cases. We also attempt to link ecological memory and resilience and illustrate how our proposed framework can be applied to forest management with an example from the hemiboreal forests of the Baltic States of Estonia, Latvia, and Lithuania. Endeavoring to emulate natural disturbances and adopt close-to-nature management, restore ecological integrity to degraded ecosystems, or adapt to altered climates requires an understanding of historical events that left an imprint on the landscape (Kirby and Watkins 1998, Swetnam et al. 1999, Bradshaw and Sykes 2014). Legacies of past events and ecosystem conditions collectively have been termed “ecological memory” (Peterson 2002, Johnstone et al. 2016). Ecological memory is the combination of species, their interactions, and structures that can guide ecosystem reorganization following disturbance (Bengtsson et al. 2003, Ogle et al. 2015). In our expanded conceptualization, ecosystem memory includes the legacies from the three levels of disturbances.

ECOSYSTEM LEGACIES

An ecosystem legacy is a physical, biological, or chemical condition (or combination of conditions) of a “previous” ecosystem element that persists long term after a disturbance. Ecosystem legacies have been described in terms of natural disturbance, biota, soil, or land-use change

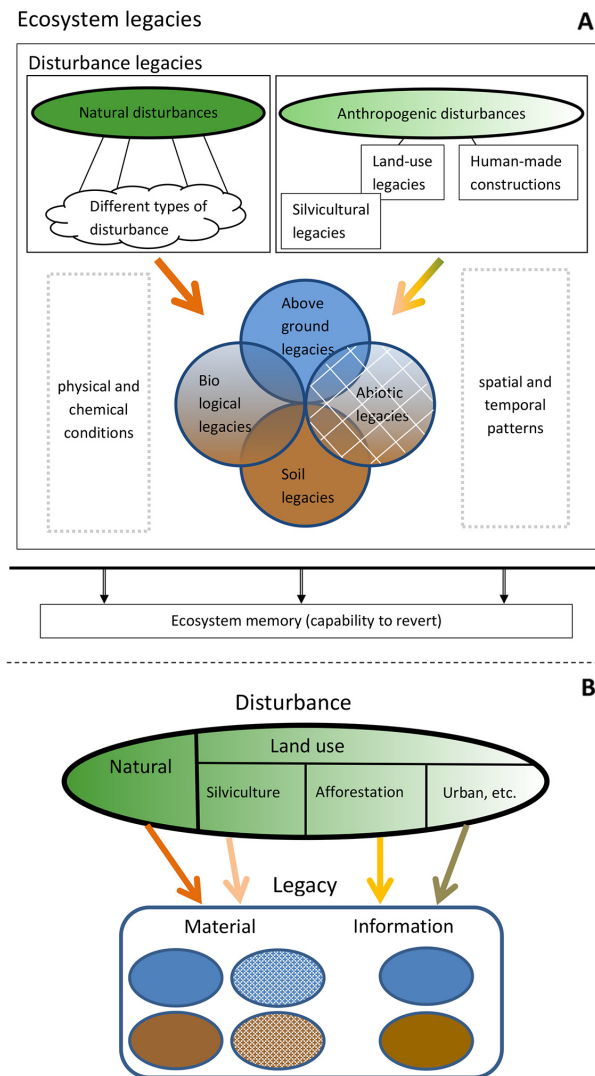


Fig. 1. Conceptual diagram of relationships between disturbances and legacies. Disturbance oval: Shades of green represent naturalness gradient in the disturbance regime. Legacy box: brown, belowground; blue, above-ground; solid fill, biotic; pattern fill, abiotic. Part (A)—representation of conventional legacy definitions, portraying significant overlap. Part (B)—proposed new classification of relationships. The six ovals represent six categories of legacies in the proposed classification. The four arrows represent different “legacy syndromes” due to differential editing and conditioning of the legacy by a given disturbance regime.

(Fig. 1A). Our use of disturbance differs from the definition of Pickett and White (1985) of disturbance as an abrupt event in time; we include gradually increasing, or ramp, events such as severe drought, extreme temperatures, fire suppression, ungulate herbivory, or pest outbreaks. Ecosystem legacies often impose major impact on the trajectory of stand or ecosystem development, including response to a contemporary

disturbance (White and Jentsch 2001). Legacies can exist at the sub-stand or microscale (e.g., tip-up mounds), stand scale (e.g., stand composition), or landscape scale (e.g., stand age distribution; Table 1). Further, ecosystem legacies can result from natural or anthropogenic (e.g., land-use change or silvicultural interventions) disturbances or their interactions (Fig. 1A). Legacies of previous disturbances may have positive or

Table 1. Classification of legacy components and disturbance characteristics relevant (+) or not relevant (–) at a specific scale in disturbed and managed forest ecosystems (based on Franklin et al. 2002, 2007).

Disturbance component	Scale of legacy component or disturbance characteristic		
	Microscale	Stand scale	Landscape
Forest disturbance characteristic			
Disturbance type	+	+	+
Disturbance severity	–	+	+
Material legacies			
Snags, stumps	+	–	–
Down logs	+	–	–
Undisturbed forest floor	+	–	–
Root mounds	+	–	–
Seedbed	+	–	–
Large living trees	+	+	–
Intact tree regeneration layer	+	+	–
Information legacies			
Composition	–	+	+
Disturbance structure†	–	+	+
Patch structure	–	–	+
Landscape age distribution	–	–	+

† Arrangement of microscale legacies at larger spatial scales.

negative effects on stand development trajectories, in terms of meeting management objectives for future stand conditions (Bengtsson et al. 2003, Foster et al. 2003). From an ecological perspective, some descriptions cast legacies as positive factors, essentially remnants of more natural or more developed states that existed prior to disturbance that condition the response to a current disturbance toward a return to the pre-disturbance state (Franklin et al. 2000). These biological legacies represent adaptations to previous disturbance regimes and shape responses to a contemporary disturbance event (Johnstone et al. 2016). In other contexts, legacies are treated as negative factors, such as degraded conditions that persist as obstacles to recovery to the pre-disturbance condition (e.g., land-use legacies sensu Foster et al. 1998, 2003). Understanding the role of legacies is necessary for designing management techniques that contribute to maintaining resilience (Franklin et al. 2007).

Disturbance legacies

A disturbance legacy (Reinhart and Callaway 2006) is the residual effect on ecosystem properties of an abiotic or biotic natural disturbance (Fig. 1A). It refers both to the pre-disturbance ecosystem remnants and to the rearrangement, repositioning, and patterns in these remnants brought about by the disturbance event. The intensity of disturbances and the severity of their effects differ (White and Jentsch 2001), thereby leaving different patterns at the sub-stand, stand, and landscape scales defined above (Frelich 2016). These patterns (along with heterogeneity of the abiotic environment) influence spatial distributions of the remnants (hereafter discussed as biological legacies) that survive disturbance. Disturbance agents can be classified as geophysical, meteorological, hydrological, climatological, or biological (Stanturf et al. 2014a), and disturbance events can vary in frequency, duration, intensity, and spatial extent (Turner et al. 1998, White and Jentsch 2001, Seidl et al. 2011). Disturbances may be selective, meaning that a disturbance may have different effects on species, age classes, or landforms (White and Jentsch 2001, Frelich 2016). A classic example is the differential effect on trees in a windstorm; some species are more susceptible to stem breakage or uprooting, depending also upon age, height, and stand density (Peterson 2007, Gardiner et al. 2016). If effects are severe enough to cause significant value loss, they become natural disasters (Below et al. 2009). Large infrequent disturbances such as volcanic eruptions (Dale et al. 2005), earthquakes (Vittoz et al. 2001), megafires (Stephens et al. 2014), or hurricanes (Stanturf et al. 2007) vary spatially in their intensity, resulting in heterogeneous patches of surviving organisms that initiate different developmental trajectories (Turner et al. 1998).

Disturbances such as wildfire and wind storms create structures and patterns that favor particular species and affect subsequent disturbances. On the one hand, wildfire is a contagious disturbance that spreads across a landscape as it interacts with features of the landscape (Peterson 2002). Fire effects differ by spatial scale, homogenizing at small scales and creating a heterogeneous mosaic of burned and unburned patches across a landscape (Peterson 2002, Larson and Churchill 2012). The pattern of vegetation on the landscape, including species traits and age, will

be influenced by varying development in burned vs. unburned patches and affect the behavior and effects of subsequent fires (Turner and Romme 1994, Larson and Churchill 2012). On the other hand, wind storms are pulse (non-contagious) disturbances that have differential effects depending upon the vegetation composition and structure (Everham and Brokaw 1996, Gardiner et al. 2016). Tree fall pits and mounds (organically derived structures) cause patterns of microtopography that result in soil drainage and fertility differences (Beatty and Stone 1986, Ulanova 2000) that favor establishment of some species over others at fine spatial scales (e.g., Beatty 1984, Vodde et al. 2015). Similarly, also biological disturbance agents such as defoliating insects (Lovett et al. 2006), browsing ungulates (Rooney and Waller 2003, Royo and Carson 2006), and dam-building beavers (Nummi and Kuuluvainen 2013) create patterns in stand structure, affect species composition, and may increase fuel loading. For example, in Lahemaa National Park (Estonia), moose (*Alces alces*) can significantly alter tree species composition by browsing the available broadleaved tree species, which over time results in increased pine dominance (Metslaid et al. 2013). Beavers are iconic ecological engineers that can change stream hydrology and create ponds that provide habitat for waterfowl, fish, and aquatic invertebrates (Nummi and Kuuluvainen 2013). Their legacy may persist for over a century (Johnston 2015).

Other large, infrequent abiotic disturbances receive less attention, but can nevertheless have major impacts on post-disturbance processes. Volcanic eruptions causing ashfall, lahars, and lava flows; mass movements; and floods may cover large areas with harsh conditions for plant growth, reallocate soil nutrients, rearrange hydrology, or initiate erosion channels, with the effect of resetting ecosystem development, introducing elements of primary succession (Crisafulli et al. 2005, Turner and Gardner 2015).

Biological legacies

Within disturbance legacies, “biological legacies” are the remnants left by disturbances (Fig. 1A). A biological legacy (Franklin et al. 2007) is an elaboration of Clements’ concept of organic residuals (Clements 1916) that persist from a pre-disturbance ecosystem and positively

influence the recovery processes of the post-disturbance ecosystem (Franklin et al. 2000). Retaining elements such as deadwood and biologically created patterns is one leg of the three-fold pillars of ecological forestry (Franklin et al. 2007). Positive biological legacies include persistent organisms, organic matter, organically derived structures and patterns (Table 1). Many biological legacies will be strongest for a short time after a disturbance and decline in strength due to mortality or decomposition (Köster et al. 2009a, b, 2015), such as occurs with organisms and organic matter, unless pools are replenished. Some biological legacies may persist for a very long time; for example, seeds of some species remain viable in soil seed banks for decades (Bekker et al. 1998, Thompson et al. 2003).

Dead and dying trees in forest ecosystems are important habitat for many other organisms (Harmon et al. 1986, Jonsson et al. 2005). Large woody debris and finer organic remnants are important biological legacies. The lack of woody debris as a result of management can be termed a land-use legacy. Woody debris is often depleted in managed forests (Harmon et al. 1986, Franklin et al. 2002, Grove and Meggs 2003), because the relatively short rotation or cutting cycle lengths of managed stands do not allow the time needed for significant amounts of large deadwood to develop. Moreover, living but decadent trees, which are abundant in natural forests, are managed against in traditional commercial forestry (e.g., Fridman and Walheim 2000, Kruys et al. 2013), and various active techniques have been advanced for adding these structural elements into managed stands (Stanturf et al. 2014a).

Biological legacies (Franklin et al. 2000) have been more or less equated to disturbance legacies as “biologically derived legacies that persist in an ecosystem or landscape following disturbance” (Johnstone et al. 2016, p. 370). Such legacies can be further defined as information legacies or material legacies discussed above in the introduction. For example, previous silvicultural interventions (forest management) may leave biotic legacies by way of altered plant species composition. Such legacies may not be regarded as positive. For example, Dickie et al. (2014) found that legacies of invasive *Pinus contorta* on soil nutrient cycling in Australia indirectly promoted invasion of non-native grasses

and herbal plant species following removal of the *P. contorta*. Such persistent negative mechanisms are usually treated as land-use legacies (discussed below).

Soil legacies

When disturbance or biological legacies are discussed in general, authors usually contemplate the aboveground or visible legacies. Belowground soil legacies are then dedicated a separate section (Fig. 1A). As usually described, a soil legacy (Baer et al. 2012) represents a positive relict of the past (i.e., pre-disturbance conditions). Baer et al. (2012) relate loss of soil legacy to degradation; soil degradation is a decline in soil productivity and capacity to regulate environmental processes (Lal 1997). A post-mining landscape, for example, has little or no soil legacy and presents an abiotic filter (or threshold, *sensu* Stanturf et al. 2014a) to unaided recovery or to active restoration. An agricultural field or pasture has been less drastically disturbed than an open-pit mine and may retain a moderate soil legacy (Baer et al. 2012). The strength of soil legacy may determine the time required for an ecosystem to return to a pre-disturbance state, that is, the resilience of the system (Tucker et al. 1998, Grandy et al. 2012). Reduction in soil legacy by changes in the physical, chemical, and biological attributes of soil, and interactions among them, may constitute a system change or regime shift that persists for millennia (Scheffer and Carpenter 2003, Šamonil et al. 2010, Grandy et al. 2012).

Many ecosystem elements, soils in particular, exhibit hysteresis where the recovery trajectory differs from the degradation trajectory (Grandy et al. 2012). Soil properties degrade faster than they recover. Soil organic matter (SOM), for example, influences chemical reactions and fertility, water relations, and aggregate stability; loss of SOM significantly degrades a soil. The rate of SOM loss after conversion from forest to agriculture is faster under tropical than under temperate conditions; 50% of the SOM may be lost within a few years to decades (Putz and Redford 2010, Grandy et al. 2012). Recovery, conversely, requires decades to centuries. Dupouey et al. (2002) provide an example from northeastern France where deforestation and conversion during Roman occupation (1950 to 1750 YBP) caused changes in soil chemical and structural properties that persist until today. These differences are mirrored by

patterns of variation in species and plant communities caused by different intensities of former agriculture almost two millennia earlier (Dupouey et al. 2002).

Although there are numerous examples of severe soil degradation resulting from clearance of natural vegetation and conversion to row crop agriculture or pasture (Trimble 1974, Richter and Markewitz 2001, Madsen et al. 2005), or from over-grazing of semi-arid grasslands (Lal 1997, Dlamini et al. 2016), less-intensive disturbance may leave a more subtle legacy in soil by altering the spatial distribution of nutrients and increasing nutrient patchiness (Mou et al. 1993, Fraterigo et al. 2005, Boyden et al. 2012), which may be reinforced by greater plant productivity in nutrient-enriched patches (Day et al. 2003). For example, intensive mechanical site preparation to regenerate pine forests in the southern United States formerly involved raking roots and topsoil into windrows to prepare a clean site for planting (Burger and Pritchett 1988). This practice redistributed nutrients on the site, causing deficiency between the windrows, and was discontinued (Allen et al. 1990). Soil biota such as mycorrhizal fungi and nitrogen-fixing bacteria play roles in nutrient cycling and plant nutrition and other soil biota (soil-borne pathogens, herbivores, and parasites) have negative effects that help determine the likelihood of plant invasions (Reinhart and Callaway 2006) or invasibility (Dechoum et al. 2015, Guo et al. 2015). While soil biota can be soil legacies, they also may be regarded as biological legacies and may be arranged into spatial patterns as parts of disturbance legacies or land-use legacies (Fig. 1A).

Land-use legacies

The counterpart of natural disturbance is anthropogenic disturbance, linked to different forms of land use (Fig. 1A). Legacies of both groups of disturbances show significant overlap, also in the classification of legacy types, but here we will concentrate on the distinctions. Land-use legacies, created by human alteration of ecosystems (White and Jentsch 2001), are many and boundless in their variety (Foster et al. 2003). Similar to legacies of natural disturbances, land-use legacies are in essence a form of disturbance legacy that creates variability in biological, abiotic, and soil legacies across the landscape (Fig. 1A).

Most legacies from past land use are presented as having negative consequences for ecosystem structure and function. Land-use legacies persist through subsequent episodes of natural disturbances and environmental change (Foster et al. 2003). As Foster et al. (2003) noted, human activity as it affects landscapes operates at multiple spatial and temporal scales and the authors concentrated on agriculture, forestry, modification of disturbance regimes, and manipulation of animal populations (Foster et al. 2003). Many legacy effects of agriculture are imprinted on soils in terms of diminished carbon and nitrogen levels or negatively affected physical properties that limit plant growth, for example, erosion and loss of the A horizon from intensive row cropping (e.g., Trimble 1974), which may be seen as a loss of soil legacy (Baer et al. 2012). Ancient societies such as the Maya of Mesoamerica dramatically altered ecosystems at multiple scales by deforestation, altered hydrology, and urban structures. Remnants of their civilization still impact forests today through reservoirs, canals, terraces, and sedimentation (Beach et al. 2015). Similarly, there is evidence of human influence on Amazonian forests especially from enrichment of preferred species and wildlife depletion near occupation sites (Bush et al. 2015).

Human manipulation of wild and domestic animals may create land-use legacies through intentional or inadvertent manipulation. Direct predation (i.e., hunting), introductions (e.g., domestic cattle, dogs, rats), and habitat manipulation (primarily by fire) are ways in which early humans may have caused declines of native mammals. Causes of late-Quaternary extinctions in the Americas and Australia have been attributed to climate change, humans, or both (Wroe and Field 2006, Gill et al. 2009, Lorenzen et al. 2011, Rule et al. 2012). Human migrations into Oceania and North and South America have coincided with widespread defaunation of megafauna (keystone carnivores and/or their prey) that created a cascade of ecological consequences of persistent effects on landscape structure, composition, and functions (Barnosky et al. 2016).

The complex interactions over time of land-use legacies can be illustrated by human impacts on native ungulates in North America. Trade in the skins of the white-tailed deer (*Odocoileus virginianus*) in early colonial times (~1600–1800)

practically eliminated deer from the colonies as the trade became commercialized (e.g., Usner 1998). Changing fashion, logging of old forests that created new habitat, and regulation of hunting caused deer populations to rebound to high densities to the extent that overbrowsing has drastically changed plant communities and created a browse legacy (Horsley et al. 2003, Rooney and Waller 2003, Royo et al. 2010). In some cases, this may lead to the dominance of a less palatable species, resulting in the formation of a dense ground vegetation layer that inhibits tree regeneration (Royo and Carson 2006). Combined with altered fire regimes and introduced pests, over-abundant white-tailed deer contribute to continuing decline of *Quercus* spp. (Morin and Liebhold 2015).

Manipulation of populations of other mammals has created legacy effects on landscapes. The American beaver (*Castor canadensis*) was locally extirpated by trapping for the fur trade during the European settlement of North America (Naiman et al. 1988). Beaver populations have recovered and recolonized most of the former range during the 20th century.

Silvicultural legacies

We distinguish silvicultural legacies from land-use legacies because they result from manipulation within a land use, rather than a change in land uses. Silvicultural systems differ in the ways trees are harvested, including the size of trees removed, size of the overstory gap, and structures maintained (Matthews 1991, Nyland 2007). The demand for forest products has changed over time, resulting in adoption of different silvicultural techniques, but legacies of former management remain in the forest. For example, the silvicultural system of coppice with standards was once widespread in many countries to supply construction material and fuelwood in rural areas that have now been replaced by industrially manufactured products (e.g., Nagaike et al. 2005, Harmer et al. 2015). Biomass has been the primary fuel for residential and industrial uses globally until replacement by fossil fuels, but continued in some industrialized countries, for example, in Korea as late as the 1960s (Lee et al. 2015). Modern management systems also leave their imprint on structure and composition of the forest, for example, shifts from shade-tolerant to shade-intolerant species,

synchronous ages tied to timing of agricultural abandonment or clearance of older forests, and depletion of deadwood noted above (Foster et al. 2003, Rhemtulla et al. 2009, Chazdon et al. 2016).

The rise of plantation forests, often of non-native species, was a notable phenomenon in the last century (Lamb 2014) although introductions in Europe, for example, *Aesculus hippocastanum* and *Castanea sativa*, date back to Roman times (Bradshaw 2004). Plantations of single, often coniferous or *Eucalyptus* species as well as afforestation of former agricultural lands have replaced naturally regenerated multispecies forests in many countries, notably *Picea abies* and *Pinus sylvestris* in northern Europe (e.g., Lindbladh et al. 2014), *Pinus radiata* in Oceania (Scott 1960), and *Eucalyptus* species throughout the tropics (Doughty 2000). *Pinus taeda* in the southern United States is a slightly different example as it is a native species that has greatly increased in dominance through natural regeneration and planting, at the expense of *Pinus palustris* and mixed pine-hardwood forests following exploitive logging of the native forests followed by fire and grazing (Carter et al. 2015). At times, these plantations have been established on soils too wet for productive agriculture, and were thus accompanied by drainage to improve timber production or in the case of afforestation, taking advantage of previous drainage for agriculture (Löhmus et al. 2015). In addition to the direct effects on soil aeration, moisture retention, peat decomposition, and subsidence, drainage impacts biodiversity (Laasimer 1981) especially of ground-layer flora, with increased risk of windthrow, fire, and pest outbreaks (Löhmus et al. 2015).

CLASSIFICATION OF ECOSYSTEM LEGACIES

As used historically, the legacy concepts discussed above (disturbance, biological, soil, land use, and silvicultural) have a lot of overlap. Disturbance legacies include land use as a type of disturbance, and silviculture is a type of land use, and all of these leave soil legacies and aboveground biological legacies. Any attempt to show the interrelationships among these is seriously confounded (Fig. 1A). However, the aforementioned new terms “material legacy” and “information legacy” (Johnstone et al. 2016) allow construction of a simple and logical six-part classification of legacies.

Material and information legacies both occur above- and belowground, and above- and belowground material legacies can be further subdivided into biotic and abiotic. This leads to four categories if we stop at the above- and belowground level of the classification tree, but six categories if we continue to the biotic/abiotic level for material legacies (Fig. 1B). One note is that all information legacies (being adaptations to disturbance regimes) are biotic and that although aboveground adaptations come to mind (e.g., thick bark, serotinous cones, easily dispersed seeds), belowground organisms or parts of organisms can also undergo natural selection to adapt to disturbance (e.g., root systems store energy to resprout and soil biota such as mycorrhizas), hence the underground information legacy category.

Furthermore, these six material and information legacies are arranged in several “legacy syndromes” which are distinctively edited patterns of legacy abundance and spatial patterns (at multiple scales), by disturbances that fall along a gradient of naturalness (Fig. 1B). The classification tree for these disturbance-based legacy syndromes has natural disturbances and land use as the initial division. Land use could be further subdivided along a naturalness gradient with subcategories (from most to least natural) including silviculture, agriculture (in the case of forests, afforestation of former agricultural land), suburban development, highly built/paved dense urban areas, and mine spoils. Note that only the first two subcategories are in the scope of this paper and considered in detail. The natural disturbance legacy syndrome could include many disturbance types considered as a whole (as shown in Fig. 1B), or could be subdivided by disturbance regime (e.g., fire vs. wind).

With this new classification, disturbances are the overall editors and spatial arrangers, of material and information legacies. They also condition the post-disturbance response of the material and information legacies—fulfilling parts of the old concepts of soil legacies (e.g., post-disturbance soil pH, nutrient status, and mycorrhizal community) and disturbance legacies (e.g., post-disturbance coarse woody debris, seedbed characteristics, distances to seed sources). The editing, conditioning, and inhibiting roles of disturbances are discussed below. This new classification also has the advantage of being stated in positive terms, rather than

a mixture of positive and negative like the historical uses of legacy terms—all legacy categories describe what passes through the filter caused by disturbance, rather than what was lost—although one can still make comparisons before and after disturbance to assess what was lost. Finally, the classification forms a logical cross-walk from legacies to resilience, novelty, and categories of forest management (see the Baltic Forest Case Study below)—with natural disturbance, silviculture, and afforestation of agricultural lands—as categories with differing legacy syndromes and levels of novelty and resilience.

ECOSYSTEM MEMORY, RESILIENCE, AND NOVELTY

The totality of information and material legacies comprises ecosystem memory, the degree to which ecological processes are shaped by remnants of previous ecosystems and past modifications of a landscape (Peterson 2002, Schaefer 2009, Johnstone et al. 2016). The expression of ecosystem memory reflects combinations of legacies and their interactions with current conditions and drivers. Besides legacies and the past disturbance events that caused a rearrangement or repositioning of these legacies, the life history traits of concurrent species determine the impact of previous events and ecosystem characteristics on future processes. Ecosystem memory is also affected by antecedent and present conditions and processes, including stressors, and by future conditions such as climate change.

Ecosystem memory has characteristics of length and strength (Ogle et al. 2015). The *length* of ecosystem memory refers to the persistence of the effect of antecedent conditions on current processes, which may range from days or weeks to centuries or millennia. Clearly, persistence of material legacies such as coarse woody debris declines over time (unless renewed) because it decomposes. Abiotic legacies such as soil structure of a B-horizon exposed by erosion may persist for centuries. The *strength* of ecosystem memory implies how significant the impact of pre-disturbance conditions is, regardless of the time since disturbance, in the sense of its importance for shaping current processes (Ogle et al. 2015). Strength of ecosystem memory, therefore, is relative to the ability of a current disturbance to

“overrule” the memory of past disturbances (Peterson 2002). Ecosystems dominated by fluctuations in external drivers such as climate change may develop novel conditions regardless of ecosystem memory (Williams and Jackson 2007).

Natural and anthropogenic disturbances exert great impact on ecosystem memory and the role of a disturbance, by means of its legacies, may be to act as an editor, inhibitor, or conditioner (White and Jentsch 2001, Foster et al. 2003). In the editor role, a disturbance acts by removing or retaining material legacies; editing could apply to species, propagules, and other biological legacies. Disturbances as editors can create irreversible conditions such as extinction of keystone species, dominant species, or ecosystem engineers. Extirpations are localized and reversible, in that animals or plants may recolonize or be re-introduced; presumably the ecological effects of floral or faunal extirpation are reversible if the extirpated organisms are re-introduced, as well. For example, large mammalian herbivores such as elephants strongly affect the flora of tropical savannas and near extirpation of grazing and browsing mammals in a protected area in Mozambique during a 35-yr civil war resulted in release of woody species and woodland expansion into the savanna (Daskin et al. 2016). Monitoring the response as mammal populations recover will reveal whether woody encroachment persists. Conversely, loss of large mammalian frugivores through hunting may have locally irreversible impacts on native flora of large-seeded trees (Bello et al. 2015). New genetic techniques with the potential to reverse extinctions have led to speculative proposals to “re-wild” landscapes with extinct and extirpated species (Donlan et al. 2006, Navarro and Pereira 2012, Sherkow and Greely 2013, Bradshaw and Sykes 2014, Nogués-Bravo et al. 2015).

Disturbance may play an inhibitor role by its material legacies. For example, a highly degraded soil may have one or more physical or chemical inhibitors including little or no organic matter, low fertility, phytotoxicities, or compacted horizons that can limit recolonization by native plants. An abandoned pasture, in contrast, may have biotic inhibition because it simply is beyond the effective dispersal distance of the native flora and requires afforestation that includes site preparation and control of competing vegetation

(Stanturf et al. 2014a, b). Overcoming inhibitions may involve indirectly intervening to alter degraded conditions and restore native communities such as the catalytic effect of exotic plantations on former mined land sites (e.g., Parrotta et al. 1997) or agricultural fields (e.g., Stanturf et al. 2007).

Disturbances can have a conditioning role by creating landscape patterns of information legacies (vegetation structure or composition) that affect susceptibility to future disturbances (e.g., wind, fire, water, mass movement, herbivores, or insects). DeRose and Long (2014) describe how structure and composition affect disturbance severity of wildfire in dry conifer forests in the western United States. At the stand scale, thinning and fuel reduction treatments can alter fire behavior (Skinner and Ritchie 2008) but the effects are short term and small scale (DeRose and Long 2014). Landscape conditioning may be accomplished by strategically placing stand-level treatments that slow the rate of fire spread (Finney 2005, Ager et al. 2010). In unmanaged landscapes, prior to a century of fire suppression, low-density stands of diverse composition conditioned the landscape to low-intensity surface fires that rarely became high-intensity crown fires (Moore et al. 1999).

Ecosystem memory may vary over spatial and temporal scales (Ogle et al. 2015). For example, climate exerts a profound influence on vegetation assemblages and legacies of past climates may persist for millennia (e.g., Svenning and Skov 2007). Climate variability may induce legacy effects (Jackson 2013), and abrupt change in climate can force changes in species distributions (Jackson et al. 2009). At localized scales, interacting disturbance legacies may pattern habitats. For example, if a Northern Hardwood forest with patches of sugar maple and hemlock (*Acer saccharum* and *Tsuga canadensis*) is blown down, those patches will regenerate with the same species due to advance regeneration matching the composition of the pre-disturbance overstory. If the blowdown is followed by a fire, the burned patches will regenerate with birch and aspen (*Betula* spp. and *Populus tremuloides*) and remain as birch and aspen, thus losing the memory of the hemlock and maple patches. Although the forest could still succeed back to hemlock and maple (dispersing from unburned patches), the patch configuration will likely differ.

Memory can be lost at a higher spatial level. To continue the Northern Hardwood example, if non-native earthworms invade (a novel element) or the ecosystem is cleared and farmed, then the memory strength declines (Fig. 2) to a level where the forest cannot return to the previous successional system that was characterized by memory loss in patches that alternated back and forth between birch–aspen and hemlock–maple, with less consequence for the overall forest. Projections are that the current sugar maple and hemlock forests will become red maple (*Acer rubrum*) forests with *Carex* spp. understories due to differing filters on species success in a warming climate: deer, earthworms, and perhaps novel climate (Frelich et al. 2012). Thus, the memory of the current maple–hemlock forest will be totally lost due to earthworm reengineering the soil (loss of the O horizon, lower nutrient status, and higher bulk density), and selective browsing and high deer numbers.

Ecosystem memory is a component of ecological or ecosystem resilience: The greater the strength of ecosystem memory, the more resilient a particular community or ecosystem (Fig. 2; Bengtsson et al. 2003, Elmqvist et al. 2003) to a particular disturbance (i.e., of what to what; Carpenter et al. 2001, DeRose and Long 2014). Resilience has been debated frequently, and many different definitions were proposed (Grimm and Wissel 1997, Newton and Cantarello 2015). We refer to the common definition of ecological resilience as the amount of disturbance that a system can absorb before changing to another stable state (Gunderson 2000, Brand and Jax 2007). Natural disturbances, as part of the natural disturbance regime, are expected to generally shift the system up or down the natural successional and stand development trajectories inherent to the forest type; that is, fluctuations in species composition do not constitute alternative states (Drever et al. 2006). Notwithstanding, there are exceptions when slowly changing environmental conditions such as paludification or sedimentation alter the site (Drever et al. 2006).

Resilience is usually posited as a desirable emergent property and increasingly included in environmental policy (Newton and Cantarello 2015). To the contrary, socially or economically undesirable conditions can be quite resilient, for example, degraded ecosystems captured by

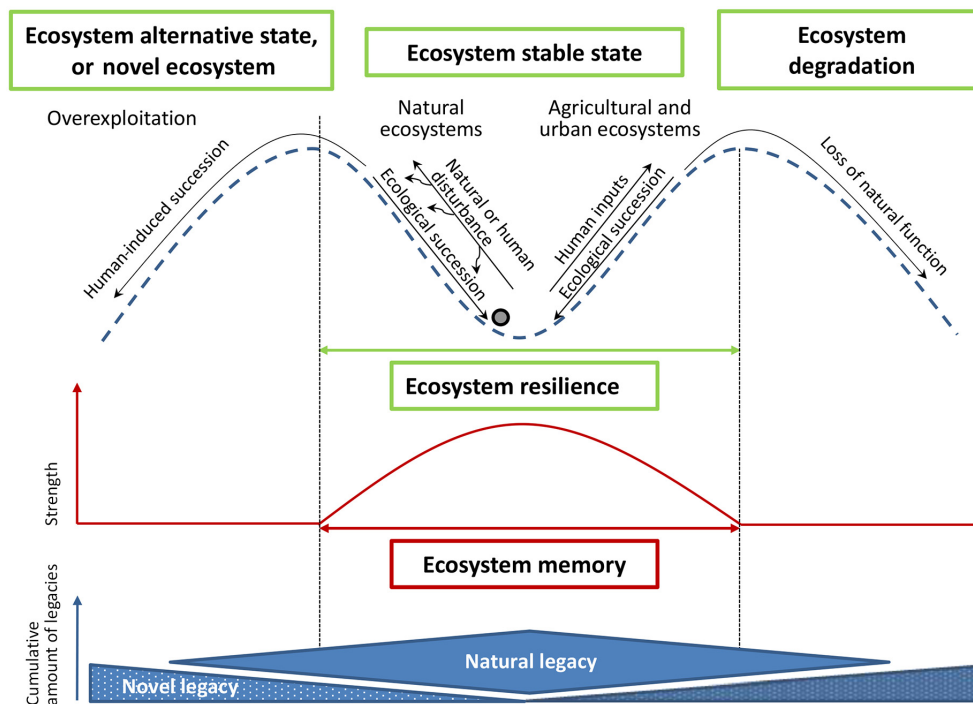


Fig. 2. Adapted from Marten (2001). Ecosystem stability and its dependence on natural and human interferences, affecting ecosystem resilience, ecological memory, and legacies. The current location of the ecosystem, represented by the gray ball, is arbitrary.

invasive species such as exotic grasses (D'Antonio and Vitousek 1992). Human interventions that alter the dynamics of a system, for example, by increasing the frequency or intensity of disturbances beyond the capacity of normal recovery processes, can create novel conditions that result in novel ecosystem responses, so-called regime shifts (Drever et al. 2006). Similarly, altering ecosystem memory by removing material or information legacies can result in regime shifts following disturbance (Fig. 2). Disturbances, in the conditioning role, may have a positive effect on ecosystem resilience when natural disturbance regimes are maintained. The effect may be negative when resilience is seriously diminished.

Novelty in ecosystems is ubiquitous but the degree of novelty varies, as does the definition of what constitutes novelty (Hobbs et al. 2013, Radeloff et al. 2015). According to Hobbs et al. (2013), a disturbed ecosystem that can revert to a former historical state if the disturbance abated is a hybrid ecosystem, whereas an ecosystem that does not revert is a novel one. Radeloff et al.

(2015) propose moving beyond categorical definitions of novel ecosystems and regard novelty as a degree of dissimilarity to historical or current conditions in one or more dimensions. In contrast to the Hobbs et al.'s (2013) formulation, novelty does not require human agency or irreversibility. Notwithstanding, novelty does not equate to change. By either definition, it seems likely that low strength of ecosystem memory increases susceptibility to novel conditions arising (Fig. 2).

An understanding of how information and material legacies contribute to ecosystem memory and affect responses to disturbance is critical to success in forest management, forest landscape restoration, and adaptation to climate change. How to manage and restore forests today to be adaptive to future conditions must be decided under great uncertainty and rapidly changing environmental conditions and social expectations (Dumroese et al. 2015, Stanturf 2015). Extreme meteorological events are expected to intensify and become more frequent as a consequence of

Table 2. Ecosystem legacy syndromes and possible management responses for four prevailing categories of forest stands in the Baltic States based on initial stand condition and ecosystem memory vs. management response and resulting novelty.

Stand condition →	Legacy syndrome		← Possible management responses
	Ecosystem memory	Novelty	
Natural disturbance	+	–	Passive management
Salvage after natural disturbance	+	–	Legacy management, suppress novelty
	–	+	Remove legacies, introduce novelty
Traditional silviculture	+	–	Natural regeneration, more broadleaves
	–	+	Conventional conifer plantations
Abandoned farmland	–	–	Afforestation, native species in mixtures
	–	+	Afforestation, native or exotic monocultures
	–	–/+	Passive restoration, novelty depends on available seed sources

altered climate (Cai et al. 2014, Leadley et al. 2014, Seidl et al. 2014), and management responses to disturbances, such as salvage logging and restoration/reforestation, will affect maintenance of legacies that are important for structuring resilient ecosystems (Franklin et al. 2007).

BALTIC FOREST CASE: THREE CLASSES OF HUMAN INTERVENTIONS IN ECOLOGICAL MEMORY

Resilience of forest ecosystems depends on the nature of disturbance including silvicultural interventions in managed systems. Legacies can affect the processes of recovery following disturbance as discussed above (editing, inhibiting, or conditioning). Although one may assume that natural forests within large uninhabited areas demonstrate dynamics not affected by human activity, the reality is that industrial activities and land management have altered natural conditions in every forest globally through long-range transport of pollutants into pristine areas and direct manipulations locally (Sanderson et al. 2002, Kareiva et al. 2007). The Baltic States in northeastern Europe (Estonia, Latvia, and Lithuania) are in the transition between boreal and temperate domains (Hytteborn et al. 2005) as they are situated at 56–59°N; 24–26°E. The region is regarded as a hemiboreal (Ahti et al. 1968) or boreo-nemoral (Sjörs 1963, Lindbladh 1999, Hytteborn et al. 2005) zone; however, southern Lithuania belongs to the temperate zone (Fig. 2).

Land-use practices and land-use change pose a gradient of altered ecosystems, starting with urban greenery and ending with uninhabited

areas in boreal Canada or Siberia. The hemiboreal forest of the Baltic States is in the middle of this gradient and is comprised of a fine-scale mosaic created by land and water management. Ecosystem memory and understanding legacies of ecosystems suggest criteria with which to evaluate forestry practices and guide future management (Laarmann et al. 2009, 2013, Swanson et al. 2011).

Humans have manipulated forest ecosystems in the Baltic States and affected vegetation dynamics, including clearance for agriculture and later abandonment as well as altering structure and composition of the forest (Jögiste 1998, Terauds et al. 2011). Land management interventions vary depending on the desired commodity or condition but all share the common feature that they affect ecosystem memory by manipulating ecosystem legacies. The range of land uses in the Baltic States suggests divisions into legacy syndromes according to management impact. We have divided these interventions into three classes (Table 2) that vary with respect to degree of ecosystem memory and novelty arising from management:

1. Altering legacies of natural disturbances (salvage logging);
2. Conventional forestry (silviculture);
3. Reconstruction of forest ecosystem after deforestation, agricultural use, and abandonment (afforestation).

In addition, forests subject only to natural disturbances are included, even though they occupy a small proportion of the landscape, because they are the logical endpoint of the gradient in naturalness and serve as reference ecosystems.

Table 3. Ecosystem legacy syndrome according to prevailing natural disturbance in managed forest and natural forest is determined by two gradients and consists of origin and mode components.

Legacy syndrome	Gap dynamics	Intermediate severity	Stand replacing
Natural disturbance	N_c	N_{ce}	N_e
Salvage	S_c	S_{ce}	S_e
Silviculture	S_c	S_{ce}, L_{ce}	S_e, L_e
Afforestation	L_c	L_{ce}	L_e

Notes: Origin: natural (N), silviculture (S), land use (L). Mode: continuous (c), episodic (e), indicated as index.

Manipulated legacies with moderately good ecosystem memory and hybrid ecosystems (Tables 2, 3) are predominant in today’s managed forests in the Baltic States (Anonymous 2014), although there is also a substantial proportion of afforested land with low ecosystem memory, artificial legacies, and novel ecosystems. Cleaning up disturbed areas and salvaging timber is a common practice; the value of salvaging is debated, however, because shade-intolerant species may subsequently prevail and delay successional development (Parro et al. 2009, 2015, Swanson et al. 2011).

When documented records enable a description of the historical changes, the patterns revealed can be analyzed (Foster et al. 1998). Status of structural components of managed forest according to its origin allows classification of ecosystem legacies based on manipulative intervention (Table 3). Material and information legacies of natural origin resulting from natural disturbances and which are not affected by human activities remain natural legacies (N). Ecosystem legacies resulting from interventions (e.g., forestry operations like timber harvesting or salvage), and originating from previous (possibly also pristine) forest, are manipulated legacies (silviculture, S) often by removal of ecosystem components. Legacies resulting from agricultural abandonment and afforestation (i.e., originating from a vegetation type spatially or temporally separated from what would have been present without human intervention) are artificial (land use, L), which means that they have a completely different impact on ecosystem memory. Further characteristics of ecosystem legacy status can be determined by the mode of temporal pattern of disturbances: continuous (index c) and episodic (index e) (Table 3, Fig. 3).

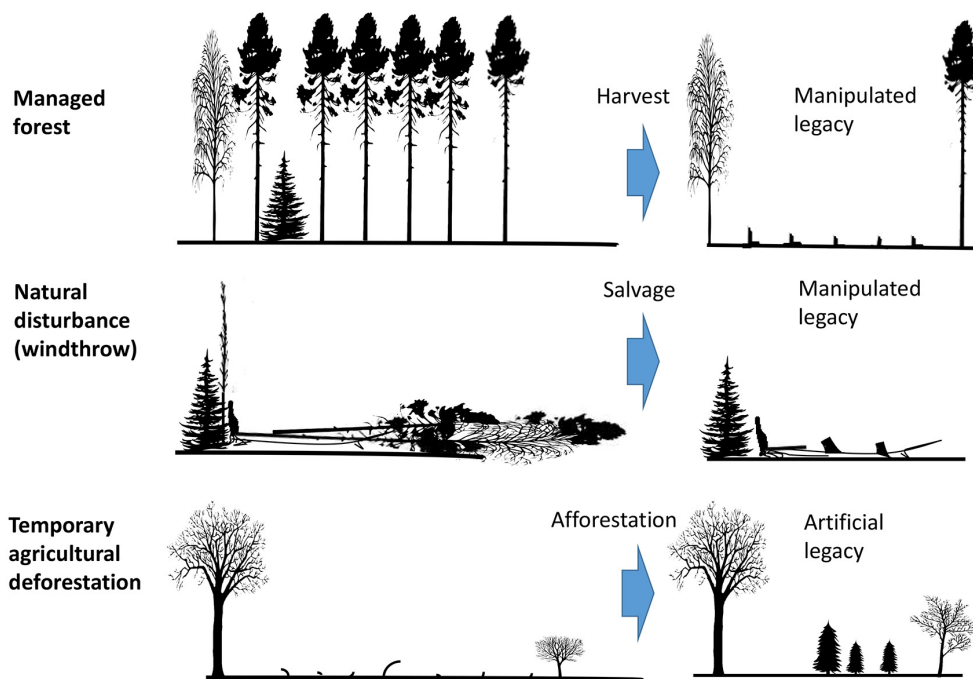


Fig. 3. Three main scenarios of manipulation of ecosystem legacies.

Timber harvest takes place in forests of different status (e.g., public or private ownership, production, or protection objectives) but the resulting characteristic traits depend on the historical treatments and contemporary harvest technique. Salvage harvesting is often carried out with technology similar to clearcuts: Trees are cut and stumps left in the forest. However, the microtopography of the clearcut salvage area is usually more heterogeneous than a regular clearcut and diversifies composition of the tree stand during spontaneous regeneration (Parro et al. 2015, Vodde et al. 2015). The challenge for foresters is the adoption of methods that are able to cope with future demands.

Forest management practices that emulate natural disturbances have been advanced as a way to increase resilience and cope with the rapidly changing global environment and the multitude of development pressures on forests (e.g., Attiwill 1994, Drever et al. 2006, Franklin et al. 2007, Kuuluvainen et al. 2015). Many authors have focused on the positive role of biological legacies and diversity of composition and structures at the stand and landscape scales (Franklin et al. 2000, Millar et al. 2007, Stanturf et al. 2014a, Frelich 2016). Other legacies, particularly those from past land use, place constraints on management (e.g., Foster et al. 1998, 2003) and condition responses to new management techniques (e.g., Spathelf et al. 2015). Efforts are underway in many countries to shift management of publicly owned forests toward nature-based (Larsen 2012, Brang et al. 2014, Kuuluvainen et al. 2015) or natural disturbance-based management (Drever et al. 2006, Bose et al. 2014). Ecosystem legacies, both material and information, affect the trajectory of stand or ecosystem development following disturbances; further manipulations associated with forest management create legacy syndromes (Fig. 3) that further differentiate ecosystem memory. Although the climate and environment change add a contingency aspect, the material and information legacies comprising ecosystem memory can be a significant determinant in the dynamic variability of ecosystem reorganization following disturbance.

ACKNOWLEDGMENTS

We are most grateful to Barbara Scott Murdock and Gordon Murdock for comments on the early version of

the manuscript. Piret Trei did most of the work with technical edition. We thank two anonymous reviewers for their constructive comments. This study was supported by a grant from the Estonian Environmental Investment Centre and by the Estonian Ministry of Education and Research Grant SF0170014s08, by institutional research funding IUT (IUT21-4) of the Estonian Ministry of Education and Research, by the Estonian Research Council Grant PUT (PUT715). Considerable amount of work was done in the frame of FORDIS-MAN network, the activity of which was financed by SNS-EFINORD. The grant to Kalev Jõgiste from Metsämiesten säätiö is acknowledged.

LITERATURE CITED

- Ager, A. A., N. M. Vaillant, and M. A. Finney. 2010. A comparison of landscape fuel treatment strategies to mitigate wildland fire risk in the urban interface and preserve old forest structure. *Forest Ecology and Management* 259:1556–1570.
- Ahti, T., L. Hämet-Ahti, and J. Jalas. 1968. Vegetation zones and their sections in northwestern Europe. *Annales Botanici Fennici* 5:169–211.
- Allen, H. L., P. M. Dougherty, and R. G. Campbell. 1990. Manipulation of water and nutrients – practice and opportunity in Southern U.S. pine forests. *Forest Ecology and Management* 30:437–453.
- Anonymous. 2014. Yearbook forest 2013. OÜ Paar, Tartu, Estonia.
- Attiwill, P. M. 1994. The disturbance of forest ecosystems: the ecological basis for conservative management. *Forest Ecology and Management* 63:247–300.
- Baer, S. G., L. Heneghan, and V. T. Eviner. 2012. Applying soil ecological knowledge to restore ecosystem services. Pages 377–378 in D. H. Wall, R. D. Bardgett, V. Behan-Pelletier, J. E. Herrick, T. H. Jones, K. Ritz, J. Six, D. R. Strong, and W. H. van der Putten, editors. *Soil ecology and ecosystem services*. Oxford University Press, Oxford, UK.
- Barnosky, A. D., E. L. Lindsey, N. A. Villavicencio, E. Bostelmann, E. A. Hadly, J. Wanket, and C. R. Marshall. 2016. Variable impact of late-Quaternary megafaunal extinction in causing ecological state shifts in North and South America. *Proceedings of the National Academy of Sciences of the United States of America* 13:856–861.
- Beach, T., S. Luzzadder-Beach, D. Cook, N. Dunning, D. J. Kennett, S. Krause, R. Terry, D. Trein, and F. Valdez. 2015. Ancient Maya impacts on the Earth's surface: An early Anthropocene analog? *Quaternary Science Reviews* 124:1–30.
- Beatty, S. W. 1984. Influence of microtopography and canopy species on spatial patterns of forest understorey plants. *Ecology* 65:1406–1419.

- Beatty, S. W., and E. L. Stone. 1986. The variety of soil microsites created by tree falls. *Canadian Journal of Forest Research* 16:539–548.
- Bekker, R. M., J. P. Bakker, U. Grandin, R. Kalamees, P. Milberg, P. Poschod, K. Thompson, and J. H. Willems. 1998. Seed size, shape and vertical distribution in the soil: indicators of seed longevity. *Functional Ecology* 12:834–842.
- Bello, C., M. Galetti, M. A. Pizo, L. F. S. Magnago, M. F. Rocha, R. A. F. Lima, C. A. Peres, O. Ovaskainen, and P. Jordano. 2015. Defaunation affects carbon storage in tropical forests. *Science Advances* 1: e1501105.
- Below, R., A. Wirtz, and D. Guha-Sapir. 2009. Disaster category classification and peril terminology for operational purposes. Centre for Research on the Epidemiology of Disasters, Munich Reinsurance Company, Brussels and Munich.
- Bengtsson, J., P. Angelstam, T. Elmqvist, U. Emanuelsson, C. Folke, M. Ihse, F. Moberg, and M. Nyström. 2003. Reserves, resilience and dynamic landscapes. *Ambio* 32:389–396.
- Bose, A. K., B. D. Harvey, S. Brais, M. Beaudet, and A. Leduc. 2014. Constraints to partial cutting in the boreal forest of Canada in the context of natural disturbance-based management: a review. *Forestry* 87:11–28.
- Bowes, M. D., and J. V. Kruttila. 1989. Multiple-use management: the economics of public forestlands. Resources for the Future, Washington, D.C., USA.
- Boyden, S., R. Montgomery, P. B. Reich, and B. Palik. 2012. Seeing the forest for the heterogeneous trees: stand-scale resource distributions emerge from tree-scale structure. *Ecological Applications* 22: 1578–1588.
- Bradshaw, R. H. W. 2004. Past anthropogenic influence on European forests and some possible genetic consequences. *Forest Ecology and Management* 197:203–212.
- Bradshaw, R. H. W. 2005. What is a natural forest? Pages 15–30 in J. A. Stanturf and P. Madsen, editors. *Restoration of boreal and temperate forests*. CRC Press, Boca Raton, Florida, USA.
- Bradshaw, R. H. W., and M. T. Sykes. 2014. *Ecosystem dynamics: from the past to the future*. Wiley Blackwell, Chichester, UK.
- Brand, F. S., and K. Jax. 2007. Focusing the meaning(s) of resilience: resilience as a descriptive concept and a boundary object. *Ecology and Society* 12: 1–16.
- Brang, P., P. Spathelf, J. B. Larsen, J. Bauhus, A. Boncčina, C. Chauvin, L. Drössler, C. García-Güemes, C. Heiri, and G. Kerr. 2014. Suitability of close-to-nature silviculture for adapting temperate European forests to climate change. *Forestry* 87:492–503.
- Burger, J. A., and W. L. Pritchett. 1988. Site preparation effects on soil moisture and available nutrients in a pine plantation in the Florida flatwoods. *Forest Science* 34:77–87.
- Bush, M. B., C. H. McMichael, D. R. Piperno, M. R. Silman, J. Barlow, C. A. Peres, M. Power, and M. W. Palace. 2015. Anthropogenic influence on Amazonian forests in pre-history: an ecological perspective. *Journal of Biogeography* 42:2277–2288.
- Cai, W., et al. 2014. Increasing frequency of extreme El Niño events due to greenhouse warming. *Nature Climate Change* 4:111–116.
- Carpenter, S., B. Walker, J. M. Anderies, and N. Abel. 2001. From metaphor to measurement: Resilience of what to what? *Ecosystems* 4:765–781.
- Carter, M. C., R. C. Kellison, and R. S. Wallinger. 2015. *Forestry in the U.S. South: a history*. Louisiana State University Press, Baton Rouge, Louisiana, USA.
- Chazdon, R. L., P. H. S. Brancalion, L. Laestadius, A. Bennett-Curry, K. Buckingham, C. Kumar, J. Moll-Rocek, I. C. Guimarães Viera, and S. J. Wilson. 2016. When is a forest a forest? Forest concepts and definitions in the era of forest and landscape restoration. *Ambio* 45:538–550.
- Christensen, N. L., et al. 1996. The report of the Ecological Society of America committee on the scientific basis for ecosystem management. *Ecological Applications* 6:665–691.
- Clements, F. E. 1916. *Plant succession: an analysis of the development of vegetation*. Carnegie Institute of Washington, Washington, D.C., USA.
- Crisafulli, C. M., F. J. Swanson, and V. H. Dale. 2005. Overview of ecological responses to the eruption of Mount St. Helens: 1980–2005. Pages 287–300 in V. H. Dale, F. J. Swanson, and C. M. Crisafulli, editors. *Ecological responses to the 1980 Eruption of Mount St. Helens*. Springer, New York, New York, USA.
- Dale, V. H., F. J. Swanson, and C. M. Crisafulli. 2005. Disturbance, survival, and succession: understanding ecological responses to the 1980 eruption of Mount St. Helens. Pages 3–11 in V. H. Dale, F. J. Swanson, and C. M. Crisafulli, editors. *Ecological responses to the 1980 Eruption of Mount St. Helens*. Springer, New York, New York, USA.
- D’Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* 23:63–87.
- Daskin, J. H., M. Stalmans, and R. M. Pringle. 2016. Ecological legacies of civil war: 35-year increase in savanna tree cover following wholesale large-mammal declines. *Journal of Ecology* 104:79–89.

- Day, K. J., M. J. Hutchings, and E. A. John. 2003. The effects of spatial pattern of nutrient supply on the early stages of growth in plant populations. *Journal of Ecology* 91:305–315.
- Dechoum, M. S., T. T. Castellani, S. M. Zalba, M. Rejmánek, N. Peroni, and J. Y. Tamashiro. 2015. Community structure, succession and invasibility in a seasonal deciduous forest in southern Brazil. *Biological Invasions* 17:1697–1712.
- DeRose, R. J., and J. N. Long. 2014. Resistance and resilience: a conceptual framework for silviculture. *Forest Science* 60:1205–1212.
- Dickie, I. A., M. G. St John, G. W. Yeates, C. W. Morse, K. I. Bonner, K. Orwin, and D. A. Peltzer. 2014. Belowground legacies of *Pinus contorta* invasion and removal result in multiple mechanisms of invasional meltdown. *AoB Plants* 6:plu056.
- Dlamini, P., P. Chivenge, and V. Chaplot. 2016. Overgrazing decreases soil organic carbon stocks the most under dry climates and low soil pH: a meta-analysis shows. *Agriculture, Ecosystems & Environment* 221:258–269.
- Donlan, C. J., et al. 2006. Pleistocene rewilding: an optimistic agenda for twenty-first century conservation. *American Naturalist* 168:660–681.
- Doughty, R. W. 2000. The eucalyptus: a natural and commercial history of the gum tree. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Drever, C. R., G. Peterson, C. Messier, Y. Bergeron, and M. Flannigan. 2006. Can forest management based on natural disturbances maintain ecological resilience? *Canadian Journal of Forest Research* 36: 2285–2299.
- Dumroese, R. K., M. I. Williams, J. A. Stanturf, and J. B. St. Clair. 2015. Considerations for restoring temperate forests of tomorrow: forest restoration, assisted migration, and bioengineering. *New Forests* 46:947–964.
- Dupouey, J. L., E. Dambrine, J. D. Laffite, and C. Moares. 2002. Irreversible impact of past land use on forest soils and biodiversity. *Ecology* 83:2978–2984.
- Elmqvist, T., C. Folke, M. Nystrom, G. Peterson, J. Bengtson, B. Walker, and J. Norberg. 2003. Response diversity and ecosystem resilience. *Frontiers in Ecology and the Environment* 1:488–494.
- Everham, E. M., and N. V. L. Brokaw. 1996. Forest damage and recovery from catastrophic wind. *Botanical Review* 62:113–185.
- Finney, M. A. 2005. The challenge of quantitative risk analysis for wildland fire. *Forest Ecology and Management* 211:97–108.
- Foster, D. R., G. Motzkin, and B. Slater. 1998. Land-use history as long-term broad-scale disturbance: regional forest dynamics in central New England. *Ecosystems* 1:96–119.
- Foster, D. R., F. Swanson, J. Aber, I. Burke, N. Brokaw, D. Tilman, and A. Knapp. 2003. The importance of land-use and its legacies to ecology and environmental management. *BioScience* 53:77–88.
- Franklin, J. F., D. B. Lindenmayer, J. A. MacMahon, A. McKee, J. Magnusson, D. A. Perry, R. Waide, and D. R. Foster. 2000. Threads of continuity: ecosystem disturbances, biological legacies, and ecosystem recovery. *Conservation Biology in Practice* 1:8–16.
- Franklin, J. F., R. J. Mitchell, and B. J. Palik. 2007. Natural disturbance and stand development principles for ecological forestry. General Technical Report NRS-19. United States Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, Pennsylvania, USA.
- Franklin, J. F., et al. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *Forest Ecology and Management* 155: 399–423.
- Fraterrigo, J. M., M. G. Turner, S. M. Pearson, and P. Dixon. 2005. Effects of past land use on spatial heterogeneity of soil nutrients in southern Appalachian forests. *Ecological Monographs* 75: 215–230.
- Frellich, L. E. 2016. Forest dynamics: how neighborhood effects fit into a landscape ecology viewpoint. *F1000Research* 5:1–10.
- Frellich, L. E., R. O. Peterson, M. Dovciak, P. B. Reich, J. A. Vucetich, and N. Eisenhauer. 2012. Trophic cascades, invasive species and body-size hierarchies interactively modulate climate change responses of ecotonal temperate-boreal forest. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 367:2955–2961.
- Fridman, J., and M. Walheim. 2000. Amount, structure, and dynamics of dead wood on managed forestland in Sweden. *Forest Ecology Management* 131:23–36.
- Gardiner, B., P. Berry, and B. Moulia. 2016. Review: wind impacts on plant growth, mechanics and damage. *Plant Science* 245:94–118.
- Gill, J. L., J. W. Williams, S. T. Jackson, K. B. Lininger, and G. S. Robinson. 2009. Pleistocene megafaunal collapse, novel plant communities, and enhanced fire regimes in North America. *Science* 326: 1100–1103.
- Grandy, S. A., J. M. Fraterrigo, and S. A. Billings. 2012. Soil ecosystem resilience and recovery. Pages 366–376 in D. H. Wall, R. D. Bardgett, V. Behan-Pelletier, J. E. Herrick, T. H. Jones, K. Ritz, J. Six, D. R. Strong, and W. H. van der Putten, editors. *Soil ecology and ecosystem services*. Oxford University Press, Oxford, UK.

- Grimm, V., and C. Wissel. 1997. Babel, or the ecological stability discussions: an inventory and analysis of terminology and a guide for avoiding confusion. *Oecologia* 109:323–334.
- Grove, S., and J. Meggs. 2003. Coarse woody debris, biodiversity and management: a review with particular reference to Tasmanian wet eucalypt forests. *Australian Forestry* 66:258–272.
- Gunderson, L. H. 2000. Ecological resilience—in theory and application. *Annual Review of Ecology and Systematics* 31:425–439.
- Guo, Q., S. Fei, J. S. Dukes, C. M. Oswalt, B. V. Iannone III, and K. M. Potter. 2015. A unified approach for quantifying invasibility and degree of invasion. *Ecology* 96:2613–2621.
- Harmer, R., K. Watts, and D. Ray. 2015. A hundred years of woodland restoration in Great Britain: changes in the drivers that influenced the increase in woodland cover. Pages 299–320 in J. A. Stanturf, editor. *Restoration of boreal and temperate forests*. Second edition. CRC Lewis, Boca Raton, Florida, USA.
- Harmon, M. E., et al. 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research* 15:133–302.
- Hobbs, R. J., E. S. Higgs, and C. M. Hall, editors. 2013. *Novel ecosystems: intervening in the new ecological world order*. John Wiley & Sons, Chichester, UK.
- Horsley, S. B., S. L. Stout, and D. S. DeCalesta. 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. *Ecological Applications* 13:98–118.
- Hytteborn, H., A. A. Maslov, D. I. Nazimova, and L. P. Rysin. 2005. Boreal forests of Eurasia. Pages 23–99 in F. Andersson, editor. *Coniferous forests. Ecosystems of the world*. Vol. 6. Elsevier, Amsterdam, The Netherlands.
- Jackson, S. T. 2013. Natural, potential and actual vegetation in North America. *Journal of Vegetation Science* 24:772–776.
- Jackson, S. T., J. L. Betancourt, R. K. Booth, and S. T. Gray. 2009. Ecology and the ratchet of events: climate variability, niche dimensions, and species distributions. *Proceedings of the National Academy of Sciences of the United States of America* 106:19685–19692.
- Jögiste, K. 1998. How human impact is reflected in forest dynamics. Pages 145–152 in M. Hytönen, editor. *Social sustainability of forestry in the Baltic Sea Region*. Finnish Forest Research Institute, Vantaa, Finland, Research Papers, 704.
- Johnston, C. A. 2015. Fate of 150 year old beaver ponds in the Laurentian Great Lakes region. *Wetlands* 35:1013–1019.
- Johnstone, J. F., et al. 2016. Changing disturbance regimes, ecological memory, and forest resilience. *Frontiers in Ecology and the Environment* 14:369–378.
- Jonsson, B. G., N. Kruys, and T. Ranius. 2005. Ecology of species living on dead wood – lessons for dead wood management. *Silva Fennica* 39:289–309.
- Kangur, A., H. Korjus, K. Jögiste, and A. Kiviste. 2005. A conceptual model of forest stand development based on permanent sample-plot data in Estonia. *Scandinavian Journal of Forest Research* 20:94–101.
- Kareiva, P., S. Watts, R. McDonald, and T. Boucher. 2007. Domesticated nature: shaping landscapes and ecosystems for human welfare. *Science* 316:1866–1869.
- Kirby, K. J., and C. Watkins, editors. 1998. *The ecological history of European forests*. CAB International, Wallingford, UK.
- Köster, K., T. Ilisson, H. Tukia, K. Jögiste, and T. Möls. 2009a. Early effects after forest disturbance in decomposition of trees in two windthrown areas in East Estonia. *Baltic Forestry* 15:143–150.
- Köster, K., M. Metslaid, J. Engelhart, and E. Köster. 2015. Dead wood basic density, and the concentration of carbon and nitrogen for main tree species in managed hemiboreal forests. *Forest Ecology and Management* 354:35–42.
- Köster, K., K. Voolma, K. Jögiste, M. Metslaid, and D. Laarmann. 2009b. Assessment of tree mortality after windthrow using photo-derived data. *Annales Botanici Fennici* 46:291–298.
- Kruys, N., J. Fridman, F. Götmark, P. Simonsson, and L. Gustafsson. 2013. Retaining trees for conservation at clearcutting has increased structural diversity in young Swedish production forests. *Forest Ecology and Management* 304:312–321.
- Kuuluvainen, T. 2009. Forest management and biodiversity conservation based on natural ecosystem dynamics in Northern Europe: the complexity challenge. *Ambio* 38:309–315.
- Kuuluvainen, T., Y. Bergeron, and K. D. Coates. 2015. Restoration and ecosystem-based management in the circumboreal forest: background, challenges, and opportunities. Pages 251–270 in J. A. Stanturf, editor. *Restoration of boreal and temperate forests*. Second edition. CRC Lewis, Boca Raton, Florida, USA.
- Laarmann, D., H. Korjus, A. Sims, A. Kangur, and J. A. Stanturf. 2013. Initial effects of restoring natural forest structures in Estonia. *Forest Ecology and Management* 304:303–311.
- Laarmann, D., H. Korjus, A. Sims, J. A. Stanturf, A. Kiviste, and K. Köster. 2009. Analysis of forest naturalness and tree mortality patterns in Estonia. *Forest Ecology and Management* 258:S187–S195.

- Laasimer, L. 1981. Anthropogenous changes of plant communities and problems of conservation. Pages 18–31 in L. Laasimer, editor. Anthropogenous changes in the plant cover of Estonia. Academy of Sciences of the Estonian S.S.R., Tartu, Estonia.
- Lal, R. 1997. Degradation and resilience of soils. Philosophical Transactions of the Royal Society of London B: Biological Sciences 352:997–1010.
- Lamb, D. 2014. Large-scale forest restoration. Routledge, London, UK.
- Larsen, J. B. 2012. Close-to-nature forest management: the Danish approach to sustainable forestry. Pages 199–218 in J. M. Garcia and J. J. D. Casero, editors. Sustainable forest management—current research. InTech, Rijeka, Croatia.
- Larson, A. J., and D. Churchill. 2012. Tree spatial patterns in fire-frequent forests of western North America, including mechanisms of pattern formation and implications for designing fuel reduction and restoration treatments. Forest Ecology and Management 267:74–92.
- Leadley, P., et al. 2014. Interacting regional-scale regime shifts for biodiversity and ecosystem services. BioScience 64:665–679.
- Lee, D. K., P. S. Park, and Y. D. Park. 2015. Forest restoration and rehabilitation in the Republic of Korea. Pages 217–231 in J. A. Stanturf, editor. Restoration of boreal and temperate forests. Second edition. CRC Lewis, Boca Raton, Florida, USA.
- Lindbladh, M. 1999. The influence of former land-use on vegetation and biodiversity in the boreo-nemoral zone of Sweden. Ecography 22:485–498.
- Lindbladh, M., A.-L. Axelsson, T. Hultberg, J. Brunet, and A. Felton. 2014. From broadleaves to spruce – the borealization of southern Sweden. Scandinavian Journal of Forest Research 29:686–696.
- Lõhmus, A., L. Remm, and R. Rannap. 2015. Just a ditch in forest? Reconsidering draining in the context of sustainable forest management. BioScience 65:1066–1076.
- Lorenzen, E. D., et al. 2011. Species-specific responses of Late Quaternary megafauna to climate and humans. Nature 479:359–364.
- Lovett, G. M., C. D. Canham, M. A. Arthur, K. C. Weathers, and R. D. Fitzhugh. 2006. Forest ecosystem responses to exotic pests and pathogens in eastern North America. BioScience 56:395–405.
- Madsen, P., F. A. Jensen, and S. Fodgaard. 2005. Afforestation in Denmark. Pages 211–224 in J. A. Stanturf and P. Madsen, editors. Restoration of boreal and temperate forests. CRC Press, Boca Raton, Florida, USA.
- Marten, G. G. 2001. Human ecology: basic concepts for sustainable development. Earthscan Publications, London, UK.
- Matthews, J. D. 1991. Silvicultural systems. Oxford University Press, Oxford, UK.
- Metslaid, M., T. Palli, T. Randveer, A. Sims, K. Jõgiste, and J. A. Stanturf. 2013. The condition of Scots pine stands in Lahemaa National Park, Estonia 25 years after browsing by moose (*Alces alces*). Boreal Environment Research 18:25–34.
- Millar, C. I., N. L. Stephenson, and S. L. Stephens. 2007. Climate change and forests of the future: managing in the face of uncertainty. Ecological Applications 17:2145–2151.
- Moore, M. M., W. Wallace Covington, and P. Z. Fule. 1999. Reference conditions and ecological restoration: a southwestern ponderosa pine perspective. Ecological Applications 9:1266–1277.
- Morin, R. S., and A. M. Liebhold. 2015. Invasive forest defoliator contributes to the impending downward trend of oak dominance in eastern North America. Forestry 89:284–289.
- Mou, P., T. J. Fahey, and J. W. Hughes. 1993. Effects of soil disturbance on vegetation recovery and nutrient accumulation following whole-tree harvest of a northern hardwood ecosystem. Journal of Applied Ecology 30:661–675.
- Nagaike, T., T. Yoshida, H. Miguchi, T. Nakashizuka, and T. Kamitani. 2005. Rehabilitation for species enrichment in abandoned coppice forests in Japan. Pages 371–381 in J. A. Stanturf and P. Madsen, editors. Restoration of boreal and temperate forests. CRC Press, Boca Raton, Florida, USA.
- Naiman, R. J., C. A. Johnston, and J. C. Kelley. 1988. Alteration of North American streams by beaver. BioScience 38:753–762.
- Navarro, L. M., and H. M. Pereira. 2012. Rewilding abandoned landscapes in Europe. Ecosystems 15:900–912.
- Newton, A. C., and E. Cantarello. 2015. Restoration of forest resilience: An achievable goal? New Forests 46:645–668.
- Nogués-Bravo, D., D. Simberloff, C. Rahbek, and N. J. Sanders. 2015. Rewilding is the new Pandora's Box in conservation. Current Biology 26:R87–R91.
- Nummi, P., and T. Kuuluvainen. 2013. Forest disturbance by an ecosystem engineer: beaver in boreal forest landscapes. Boreal Environment Research 18:13–24.
- Nyland, R. D. 2007. Silviculture: concepts and applications. Waveland Press, Boston, Massachusetts, USA.
- Ogle, K., J. J. Barber, G. A. Barron-Gafford, L. P. Bentley, J. M. Young, T. E. Huxman, M. E. Loik, and D. T. Tissue. 2015. Quantifying ecological memory in plant and ecosystem processes. Ecology Letters 18:221–235.
- O'Hara, K. L. 2016. What is close-to-nature silviculture in a changing world? Forestry 89:1–6.

- Parro, K., K. Köster, K. Jögiste, and F. Vodde. 2009. Vegetation dynamics in a fire damaged forest area: the response of major ground vegetation species. *Baltic Forestry* 15:206–215.
- Parro, K., M. Metslaid, G. Renel, A. Sims, J. A. Stanturf, K. Jögiste, and K. Köster. 2015. Impact of postfire management on forest regeneration in a managed hemiboreal forest, Estonia. *Canadian Journal of Forest Research* 45:1192–1197.
- Parrotta, J. A., J. W. Turnbull, and N. Jones. 1997. Catalyzing native forest regeneration on degraded tropical lands. *Forest Ecology and Management* 99:1–7.
- Peterken, G. F. 1999. Applying natural forestry concepts in an intensively managed landscape. *Global Ecology and Biogeography* 8:321–328.
- Peterson, G. D. 2002. Contagious disturbance, ecological memory, and the emergence of landscape pattern. *Ecosystems* 5:329–338.
- Peterson, C. J. 2007. Consistent influence of tree diameter and species on damage in nine eastern North America tornado blowdowns. *Forest Ecology and Management* 250:96–108.
- Pickett, S. T. A., and P. S. White. 1985. Patch dynamics: a synthesis. Pages 371–384 in S. T. A. Pickett and P. S. White, editors. *The ecology of natural disturbance and patch dynamics*. Academic Press, New York, New York, USA.
- Pommerening, A., and S. T. Murphy. 2004. A review of the history, definitions and methods of continuous cover forestry with special attention to afforestation and restocking. *Forestry* 77:27–44.
- Puettmann, K. J., K. D. Coates, and C. C. Messier. 2009. *A critique of silviculture*. Island Press, Washington, D.C., USA, Covelo, California, USA, London, UK.
- Putz, F. E., and K. H. Redford. 2010. The importance of defining ‘forest’: tropical forest degradation, deforestation, long-term phase shifts, and further transitions. *Biotropica* 42:10–20.
- Radeloff, V. C., J. W. Williams, B. L. Bateman, K. D. Burke, S. K. Carter, E. S. Childress, K. J. Cromwell, C. Gratton, A. O. Hasley, and B. M. Kraemer. 2015. The rise of novelty in ecosystems. *Ecological Applications* 25:2051–2068.
- Reinhart, K. O., and R. M. Callaway. 2006. Soil biota and invasive plants. *New Phytologist* 170:445–457.
- Rhemtulla, J. M., D. J. Mladenoff, and M. K. Clayton. 2009. Legacies of historical land use on regional forest composition and structure in Wisconsin, USA (mid-1800s–1930s–2000s). *Ecological Applications* 19:1061–1078.
- Richter Jr., D. D., and D. Markewitz. 2001. *Understanding soil change: soil sustainability over millennia, centuries, and decades*. Cambridge University Press, Cambridge, UK.
- Rooney, T. P., and D. M. Waller. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. *Forest Ecology and Management* 181:165–176.
- Royo, A. A., and W. P. Carson. 2006. On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. *Canadian Journal of Forest Research* 36:1345–1362.
- Royo, A. A., S. L. Stout, D. S. deCalesta, and T. G. Pierson. 2010. Restoring forest herb communities through landscape-level deer herd reductions: Is recovery limited by legacy effects? *Biological Conservation* 143:2425–2434.
- Rule, S., B. W. Brook, S. G. Haberle, C. S. M. Turney, A. P. Kershaw, and C. N. Johnson. 2012. The aftermath of megafaunal extinction: ecosystem transformation in Pleistocene Australia. *Science* 335:1483–1486.
- Šamonil, P., K. Král, and L. Hort. 2010. The role of tree uprooting in soil formation: a critical literature review. *Geoderma* 157:65–79.
- Sanderson, E. W., M. Jaiteh, M. A. Levy, K. H. Redford, A. V. Wannebo, and G. Woolmer. 2002. The human footprint and the last of the wild: the human footprint is a global map of human influence on the land surface, which suggests that human beings are stewards of nature, whether we like it or not. *BioScience* 52:891–904.
- Schaefer, V. 2009. Alien invasions, ecological restoration in cities and the loss of ecological memory. *Restoration Ecology* 17:171–176.
- Scheffer, M., and S. R. Carpenter. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends in Ecology & Evolution* 18:648–656.
- Scott, C. W. 1960. Radiata pine as an exotic. *Unasylva* 14:6–16.
- Seidl, R., M.-J. Schelhaas, W. Rammer, and P. J. Verkerk. 2014. Increasing forest disturbances in Europe and their impact on carbon storage. *Nature Climate Change* 4:806–810.
- Seidl, R., et al. 2011. Modelling natural disturbances in forest ecosystems: a review. *Ecological Modelling* 222:903–924.
- Sherkow, J. S., and H. T. Greely. 2013. What if extinction is not forever. *Science* 340:32–33.
- Sjörs, H. 1963. Amphi-Atlantic zonation, nemoral to arctic. Pages 109–126 in A. Löve and D. Löve, editors. *North Atlantic biota and their history*. The Macmillan Company, New York, New York, USA.
- Skinner, C., and M. Ritchie. 2008. The cone fire: a chance reckoning for fuel treatments. *Fire Science Brief* 4:1–6.
- Spathelf, P., A. Bolte, and E. van der Maaten. 2015. Is close-to-nature silviculture (CNS) an adequate

- concept to adapt forests to climate change? *Landbauforschung* 65:161–170.
- Stanturf, J. A. 2015. Future landscapes: opportunities and challenges. *New Forests* 46:615–644.
- Stanturf, J. A., S. L. Goodrick, and K. W. Outcalt. 2007. Disturbance and coastal forests: a strategic approach to forest management in hurricane impact zones. *Forest Ecology and Management* 250:119–135.
- Stanturf, J. A., B. J. Palik, and R. K. Dumroese. 2014a. Contemporary forest restoration: a review emphasizing function. *Forest Ecology and Management* 331:292–323.
- Stanturf, J. A., B. J. Palik, M. I. Williams, R. K. Dumroese, and P. Madsen. 2014b. Forest restoration paradigms. *Journal of Sustainable Forestry* 33: S161–S194.
- Stephens, S. L., et al. 2014. Temperate and boreal forest mega-fires: characteristics and challenges. *Frontiers in Ecology and the Environment* 12:115–122.
- Suffling, R., and A. H. Perera. 2004. Characterizing natural forest disturbance regimes: concepts and approaches. Pages 43–54 in A. H. Perera, L. J. Buse, and M. G. Weber, editors. *Emulating natural forest landscape disturbances: concepts and applications*. Columbia University Press, New York, New York, USA.
- Svenning, J. C., and F. Skov. 2007. Ice age legacies in the geographical distribution of tree species richness in Europe. *Global Ecology and Biogeography* 16:234–245.
- Swanson, M. E., J. F. Franklin, R. L. Beschta, C. M. Crisafulli, D. A. DellaSala, R. L. Hutto, D. B. Lindenmayer, and F. J. Swanson. 2011. The forgotten stage of forest succession: early-successional ecosystems on forest sites. *Frontiers in Ecology and the Environment* 9:117–125.
- Swetnam, T. W., C. D. Allen, and J. L. Betancourt. 1999. Applied historical ecology: using the past to manage for the future. *Ecological Applications* 9:1189–1206.
- Tērauds, A., G. Brūmelis, and O. Nikodemus. 2011. Seventy-year changes in tree species composition and tree ages in state-owned forests in Latvia. *Scandinavian Journal of Forest Research* 26:446–456.
- Thompson, K., R. M. Ceriani, J. P. Bakker, and R. M. Bekker. 2003. Are seed dormancy and persistence in soil related? *Seed Science Research* 13:97–100.
- Trimble, S. W. 1974. Man-induced soil erosion on the Southern Piedmont. Pages 1700–1970. *Soil Conservation Society of America*, Ankeny, Iowa, USA.
- Tucker, J. M., E. S. Brondizio, and E. F. Moran. 1998. Rates of forest regrowth in eastern Amazonia: a comparison of Altamira and Bragantina regions, Para State, Brazil. *Interciencia* 23:64–73.
- Turner, M. G., W. L. Baker, C. Peterson, and R. K. Peet. 1998. Factors influencing succession: lessons from large, infrequent natural disturbances. *Ecosystems* 1:511–523.
- Turner, M. G., and R. H. Gardner. 2015. Landscape disturbance dynamics. Pages 175–228 in M. G. Turner and R. H. Gardner, editors. *Landscape ecology in theory and practice: pattern and process*. Springer-Verlag, New York, New York, USA.
- Turner, M. G., and W. H. Romme. 1994. Landscape dynamics in crown fire ecosystems. *Landscape Ecology* 9:59–77.
- Ulanova, N. G. 2000. The effects of windthrow on forests at different spatial scales: a review. *Forest Ecology and Management* 135:155–167.
- Usner Jr., D. H. 1998. *American Indians in the Lower Mississippi Valley: social and economic histories*. University of Nebraska Press, Lincoln, Nebraska and London, UK.
- Vittoz, P., G. H. Stewart, and R. P. Duncan. 2001. Earthquake impacts in old-growth *Nothofagus* forests in New Zealand. *Journal of Vegetation Science* 12:417–426.
- Vodde, F., K. Jögiste, J. Engelhart, L. E. Frelich, W. K. Moser, A. Sims, and M. Metslaid. 2015. Impact of wind-induced microsites and disturbance severity on tree regeneration patterns: results from the first post-storm decade. *Forest Ecology and Management* 348:174–185.
- White, P. S., and J. Harrod. 1997. Disturbance and diversity in a landscape context. Pages 128–159 in J. A. Bissonette, editor. *Wildlife and landscape ecology*. Springer-Verlag, New York, New York, USA.
- White, P. S., and A. Jentsch. 2001. The search for generality in studies of disturbance and ecosystem dynamics. *Progress in Botany* 62:399–450.
- White, P. S., and S. T. A. Pickett. 1985. Natural disturbance and patch dynamics: an introduction. Pages 3–13 in S. T. A. Pickett and P. S. White, editors. *The ecology of natural disturbance and patch dynamics*. Academic Press, New York, New York, USA.
- Williams, J. W., and S. T. Jackson. 2007. Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment* 5: 475–482.
- Wroe, S., and J. Field. 2006. A review of the evidence for a human role in the extinction of Australian megafauna and an alternative interpretation. *Quaternary Science Reviews* 25:2692–2703.