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

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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.

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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

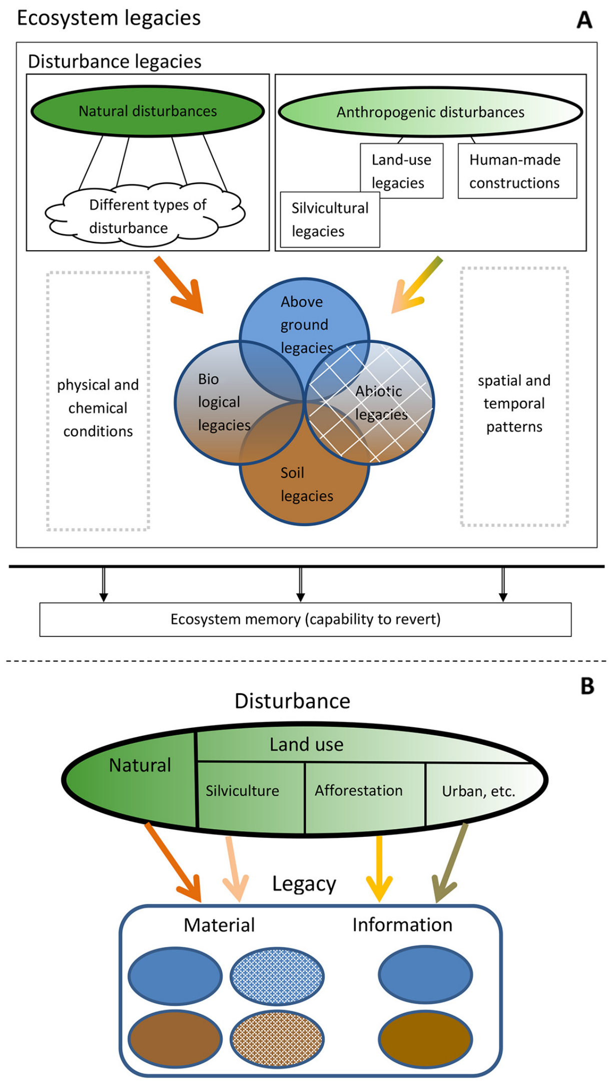

Fig. 1. Conceptual diagram of relationships between disturbances and legacies. Disturbance oval: Shades of green represent naturalness gradient in the disturbance regime. Legacy box: brown, belowground; blue, aboveground; solid fill, biotic; pattern fill, abiotic. Part (A)—representation of conventional 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. 2014*a*), 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. 2009*a*, *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. 2014*a*).

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. 2014*a*) to unaided recovery or to active restoration. An agricultural field or pasture has been less drastically disturbed than an opencast 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, Fraterrigo 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 (Lõhmus 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 (Lõhmus 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. 2014*a*, *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 predisturbance 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

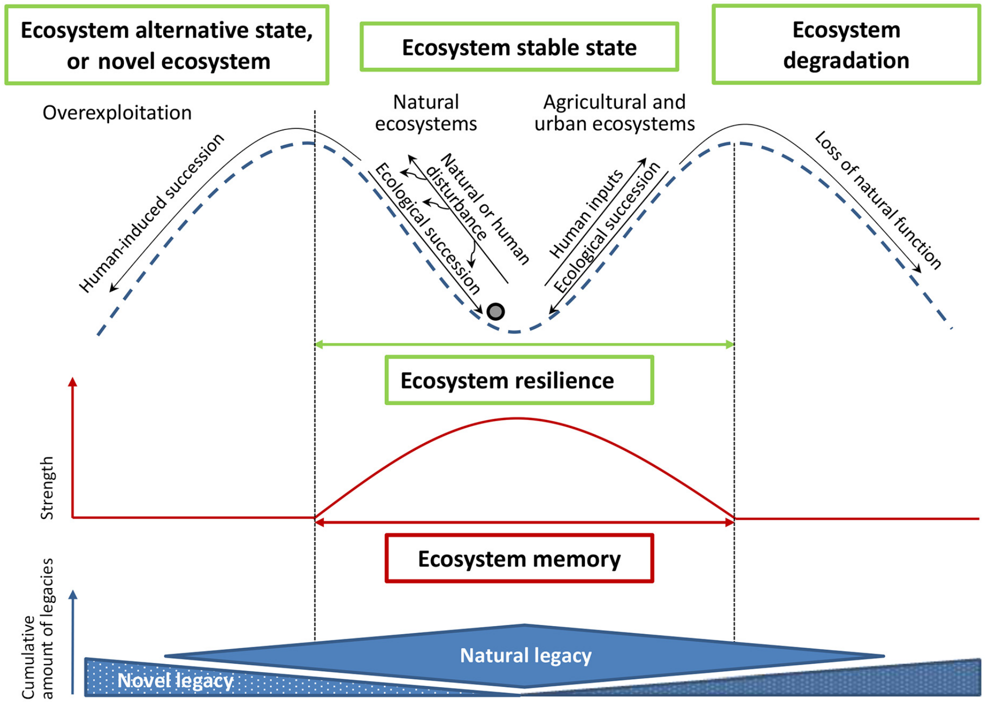

Fig. 2. Adapted from Marten (2001). Ecosystem stability and its dependence on natural and human interferences, affecting ecosystem resilience, ecological memory, and legacies. The current location of the ecosystem, represented by the gray ball, is arbitrary.

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.

	Legacy syndrome		
Stand condition →	Ecosystem memory	Novelty	← Possible management responses
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 (Jõgiste 1998, Tērauds 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).

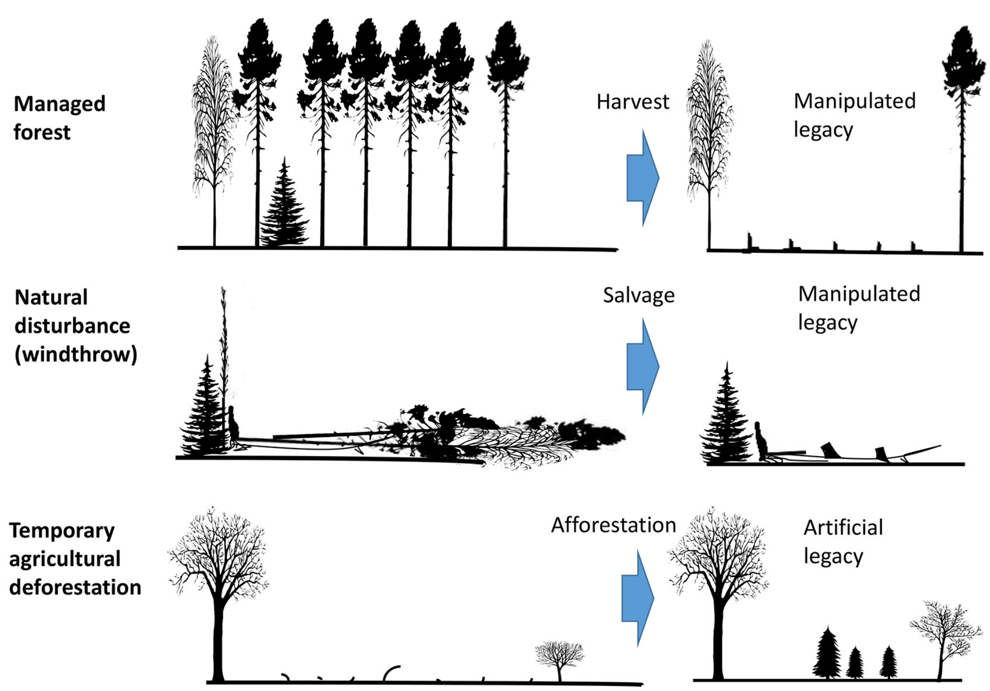

Fig. 3. Three main scenarios of manipulation of ecosystem legacies.

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. 2014*a*, 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.

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