Chapter 17
Strategies for the Ecological Restoration of the Boreal Forest Facing Climate Change

Timo Kuuluvainen and Petri Nummi

Abstract The large-scale simplification of boreal forest ecosystem structure, composition, and processes to boost timber production, combined with the increasing pressure of climate change, has created an urgent need to restore forest biodiversity and resilience. However, the issue of restoration is relatively new in boreal forests, and there are no established strategies to guide restoration planning and action. Here we provide an overview of suggested strategic concepts and approaches for boreal forest ecosystem restoration and discuss their applicability to various situations. The key strategic questions in restoration for attaining a favorable conservation status of native ecosystem types and their intrinsic dynamics in a given area are: what, how much, and when to restore? We conclude that adaptive capacity should serve as an overarching strategic framework in boreal forest restoration during times of rapid climate change.

17.1 Introduction

The boreal forest represents about one-third of the global forest, and it spreads across the boreal biome in Canada, Alaska, Russia, and Scandinavia (Kneeshaw et al., 2011). The boreal forest plays a crucial role in global climate regulation because it contains a large share of the global terrestrial carbon. This forest is vital for biodiversity, as it provides habitats for numerous species adapted to specific northern conditions (Bradshaw et al., 2009). Most boreal countries have long-standing and strong traditions in forestry education and related forest-dedicated institutions and timber-oriented forest management. They also produce a disproportionally large share of forest products for the global market (SNS, 2021).

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M. M. Girona et al. (eds.), *Boreal Forests in the Face of Climate Change*,
Advances in Global Change Research 74,
https://doi.org/10.1007/978-3-031-15988-6_17

Although unmanaged forest still exists, especially in remote high-latitude areas of the boreal zone (Gauthier et al., 2015), the southern, more productive, and naturally species-rich forests are generally heavily exploited and currently under intensive management (Burton et al., 2010). Forest utilization has been most intensive and long-lasting in Fennoscandia, especially in Sweden and Finland where natural forest mostly remains only in remote high-latitude and high-altitude areas (Kuuluvainen et al., 2017). It is evident that to reach representativeness and favorable conservation status in these countries, there is a mounting need for forest protection and restoration, especially in the southern and middle boreal zones where natural biodiversity is high (Angelstam & Andersson, 2001; Angelstam et al., 2020; Berglund & Kuuluvainen, 2021; Vanha-Majamaa et al., 2007). The situation is also similar in Canada and Russia in that the southern boreal forests have been most intensively utilized, although extensive areas of natural forest remain in more northern boreal regions (Potapov et al., 2008).

Overall, the issue of forest restoration is relatively new in boreal forests (Stanturf & Madsen, 2005). The boreal countries have traditionally focused on timber management and timber-yield sustainability (Puettmann et al. 2009). This goal is met in many boreal countries using intensive even-aged management, where wood is harvested with short clear-cutting cycles relative to the natural longevity of stand development cycles. However, such agriculture-inspired crop management practices have turned vast areas of structurally diverse natural forests into production forests; the latter are structurally and compositionally simplified and lack vital structural legacy features, such as large old trees and abundant and diverse deadwood. The large-scale simplification of ecosystem structures to boost timber production has reduced biodiversity, limited the ability of forests to deliver ecosystem services, and weakened forest resilience to perturbations (Angelstam et al., 2020; Berglund & Kuuluvainen, 2021). As climate change effects become increasingly evident, this simplification has created an urgent need for forest restoration and ecosystem management to increase resilience within large areas of the boreal forest (Burton & Macdonald, 2011; Kuuluvainen, 2009).

The extent and magnitude of change brought by intensive forestry is exemplified by the situation in Finland, where in a recent national assessment, 70% of forested habitat types on mineral soil were evaluated as threatened (constituting 49% of the country’s forest area), mostly because of the low amounts of deadwood and simplified structure of these forests (Kontula & Raunio, 2019). Such extensive degradation of forested ecosystems has taken place over most of boreal Fennoscandia within only the last 70 years (Keto-Tokoi & Kuuluvainen, 2014). Because of the inertia of forest ecosystems to environmental change, we have only seen part of the cumulative ecological effects of such large-scale alteration of northern forest ecosystem structures. Such delays in ecological responses are due, in part, to long successional sequences and long-lasting legacies from the more natural forest stages of the past, e.g., slowly decaying pools of fallen deadwood (Lilja & Kuuluvainen, 2005) and delayed population responses to habitat degradation and loss, a phenomenon known as extinction debt (Hanski, 2000).

Degradation of habitat quality and the anticipated rapid warming of climate at high latitudes threaten to accelerate biodiversity loss and boreal carbon pool depletion in the near future (Gauthier et al., 2015; Moen et al., 2014). At some point, the ecosystem may cross critical transition thresholds, resulting in large-scale ecosystem state shifts. Beyond this point, sustainable management may no longer be possible (Gauthier et al., 2015). Such ecosystem state shifts, from a closed forest to low productivity open woodland, are already evident in some parts of the boreal zone because of repeated high-severity fires (Girard et al., 2008; Jasinski & Payette, 2005).

As a response to ecosystem degradation, boreal forestry is confronted with increasing demands to restore structurally impoverished managed forests closer to their natural state of variability and complexity (Burton et al., 2010; Kuuluvainen, 2009; Messier et al., 2013). This pressure is challenging traditional forest management approaches, particularly the sustained yield paradigm of sustainability. The application of ecosystem management in boreal forestry calls for a paradigm change toward large-scale restoration and more diversified management approaches inspired by natural forest structure and dynamics (Berglund & Kuuluvainen, 2021; Burton & Macdonald, 2011).

In this chapter, we provide an overview of strategic concepts and approaches in boreal forest ecosystem restoration. We discuss under which circumstances the different approaches could be applicable and how to harness ecological knowledge in forest restoration and ecosystem management. The key strategic questions are: what, how much, and when to restore a forest to attain representativeness and continuity of native habitat types and ecological processes? However, the question of how to restore is an operational question that we do not address here. Finally, we discuss the importance of and prospects for forest restoration in the boreal zone in times of rapid climate change.

17.2 Development of Strategic Thinking in Conservation, Restoration, and Ecosystem Management

Restoration can be defined as a process aiding the recovery of degraded, damaged, or destroyed ecosystems toward their natural state. When we look into the past, it is possible to distinguish some broad developmental steps in conservation and restoration thinking, restoration concepts, and associated strategies reflecting the development of ecological science and an understanding of ecosystem structure and functioning (Fig. 17.1). The earliest strategic approach can be called *forest-as-museum*. This was founded on the Clementsian view of deterministic succession and its assumed natural and permanent static endpoint, the *climax* (Clements, 1916). According to this view, it was possible to protect or passively restore spectacular but often small remaining fragments of natural vegetation as examples of original local conditions.

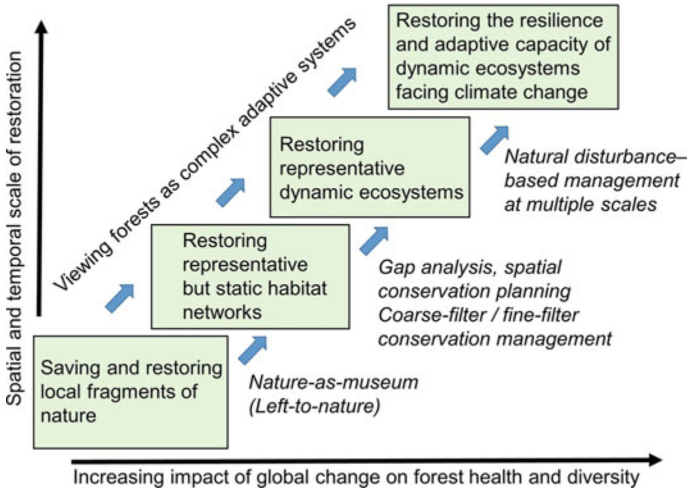

Fig. 17.1 A simplified illustration of the development of some key strategic approaches and concepts underlying forest conservation, restoration, and sustainable management. Modified with permission of Informa UK Ltd. through PLSclear from Kuuluvainen (2017)

However, because of the historical development of forest utilization and conservation, the remaining natural forest fragments are often too small and isolated to host their intrinsic dynamics and viable populations (Angelstam et al., 2020). Moreover, given the lack of proper conservation policies and planning, they are not representative of the original habitat distribution, as they are mostly forests located on marginal and remote sites of low productivity where biodiversity is naturally low (Angelstam et al., 2020; Kuuluvainen et al., 2017; Lilja & Kuuluvainen, 2005).

Such poorly connected and inadequately representative forest protection areas created a need to complement the conservation area network, where restoration of degraded forests and their connectivity played a central role (Halme et al., 2013; Ward et al., 2020); the ability of species to move between habitats was understood to be crucial for long-term viability of populations and must be taken into account in species conservation and restoration (Hanski, 2000; MacArthur & Wilson, 1967). This shift in thinking led to an emphasis on habitat quality and size, networks and connectivity, and, consequently, the spatial conservation planning necessary for ensuring a favorable conservation and viable populations within the habitats (Moilanen et al., 2011). Practical conservation measures in northern European forestry included the introduction of the landscape ecological planning framework based on the patch-corridor-matrix model (Forman 1995), the valuable key-habitat concept (Timonen et al., 2011), and retention-tree practices (Kuuluvainen et al., 2019; Simonsson et al., 2015).

With mounting concerns of the impacts of climate change on boreal forests, there has been an increased focus on dynamic properties of forest ecosystems as the basis of biodiversity conservation, ecosystem resilience, and adaptive capacity

(Bengtsson et al., 2003; Rist & Moen, 2013). This approach emphasizes the self-organized dynamic complexity of ecological systems (Levin, 1998) as a basis for ecosystem management and planning (Messier et al., 2013). Forested landscapes have been described as complex adaptive systems at multiple dynamically interacting scales (Gunderson & Holling, 2001) driven by local disturbance regimes affected by environmental fluctuations and global change (Messier et al., 2013). This view embraces the properties of complex ecological systems, such as emergent properties, self-organization, resilience, and adaptability (Filotas et al., 2014; Gunderson & Holling, 2001; Holling, 2001). This approach emphasizes the importance of the natural *adaptive cycle* in building *evolutionary resilience* (Sgrò et al., 2011) in restoration efforts and sustainable management. Interestingly, this echoes the early left-to-nature approach (Fig. 17.1) but now with a more robust ecological framework based on a novel understanding of the self-organization properties of ecosystems.

Although no overarching theory of restoration has emerged, several concepts are closely linked to and widely used in the context of ecological restoration. These include, in particular, the established concepts of (1) natural (historical) range of variation (NRV, Landres et al., 1999), (2) coarse- and fine-filter conservation management (Hunter, 1991, 1993), (3) natural disturbance emulation in forestry (Angelstam, 1998; Bergeron et al., 2002), (4) managing forests as complex adaptive systems (Messier et al., 2013), and (5) adaptive cycle and the concepts of *panarchy* (Gunderson & Holling, 2001). In the following section, we briefly explain these concepts and discuss them in relation to forest restoration with special reference to challenges brought by climate change.

17.3 Importance of Reference Conditions

Ecosystem restoration should ultimately be based on a thorough understanding of the structure and functioning of ecosystems and the habitat requirements and dynamics of species and communities. However, such knowledge of specific habitat requirements of the thousands of species living in every single forest stand is, and always will be, limited (Kuuluvainen & Siitonen, 2013). Moreover, we do not often know to which past or current conditions the species have adapted. This situation is complicated further by the possibility of rapid eco-evolutionary adaptation in some species populations (Rice & Emery, 2003; Sgrò et al., 2011). All this makes comprehensive species-by-species restoration challenging, if not impossible, and calls for more holistic approaches based on restoring habitats that emerge through the adaptive cycle.

For example, in northern Europe, boreal forests have, for the most part, been strongly transformed by a long history of intensive utilization and (more recently) by modern intensive forestry (Kuuluvainen, 2009; Linder & Östlund, 1998; Östlund et al., 1997). In this situation, knowledge of conditions characterizing boreal forest habitat types before the onset of intensive human usage is pivotal as a point of reference for conservation and restoration (Berglund & Kuuluvainen, 2021). This refers to conditions where—acknowledging that humans have to some degree probably been omnipresent in all boreal forests throughout history (Josefsson et al., 2010)—human influence has been negligible, and natural forest structure and dynamics have prevailed (Brūmelis et al., 2011).

It is worth noting that our understanding of reference conditions and their natural variation in boreal forests has been, to a large extent, revised by recent research (summarized in Berglund & Kuuluvainen, 2021). These new findings have important implications for answering the questions of what and how much to restore. For example, in boreal northern Europe, there has been a change from earlier perceptions of universal even-aged forest dynamics driven by stand-replacing disturbances toward current knowledge highlighting the role of non-stand-replacing disturbances and the resultant prevalence of old forests with complex structures and dynamics (Berglund & Kuuluvainen, 2021). A similar revision of reference forest conditions has taken place in North America (Bergeron & Fenton, 2012).

17.3.1 Natural Range of Variation and Coarse-Filter/Fine-Filter Management

The natural (historical) range of variation (NRV) concept of ecosystems provides knowledge of their past distribution, structure, and dynamics (Landres et al., 1999). This information can be used as a reference for guiding forest management, conservation, and restoration (Keane et al., 2009). The coarse- and fine-filter (CFF) approach builds upon a knowledge of NRV and separates two complementary strategies for sustaining ecosystems and their biodiversity. The coarse-filter strategy emphasizes the importance of maintaining natural ecosystem types and structures at large scales (Hunter, 1991, 1993). The assumption is that restoring or maintaining natural coarse-scale landscape conditions within a range to which the organisms are adapted will likely conserve most species and maintain sustainable ecosystems. The coarse-filter approach does not necessarily consider only reserves but rather recognizes ecological processes and the dynamic distribution of habitats across the entire landscape or region over time. The coarse-filter strategy has been recommended as a holistic approach, as it avoids the pitfalls of reductionist species-by-species planning (Table 17.1). The latter approach is also severely restricted by the lack of knowledge of ecological habitat requirements for most forest-dwelling species.

Complementary to this coarse-filter management, the fine-filter approach focuses on individual species or fine-scale elements of diversity, which are critical in conserving biodiversity and are not sufficiently accounted for by coarse-filter management. This fine-filter approach tries to safeguard, for example, those species that have very specialized habitat requirements or that do not tolerate any management actions and thus easily “fall through” the coarse filter. Thus, the fine-filter

Table 17.1 Comparison of different strategic approaches to forest conservation and restoration with indications of when a property is typical (*positive*) or not typical (*negative*) of a given restoration approach and when this relationship may be less strict (*parentheses*)

Approach	Static	Dynamic	Reductionist	Holistic	Multiple scales	Adaptive
Forest-as-museum	+	–	–	–	–	–
Coarse/fine filter	+	(–)	(+)	+	+	(+)
Disturbance-based	–	+	–	+	+	+
Adaptive cycle	–	+	–	+	+	+

approach consists of developing specific conservation strategies for specific species that are considered to be at particular risk under the coarse-filter approach. An example of a fine filter could be the provision of nesting boxes for cavity-nesting birds and mammals when cavity trees are not available, e.g., because of forest management actions.

The applicability of the coarse-filter/fine-filter approach depends on adequate knowledge of the past natural or historical conditions. Because of the long-term human impact, the protected forest fragments available as references may not be representative and large enough to harbor natural ecosystem structures, dynamics, and viable species assemblages (Lilja & Kuuluvainen, 2005; Nordén et al., 2013). In some cases, the system may have moved too far from its natural state to restore it to any past state (Hobbs et al., 2009; Jackson & Hobbs, 2009).

Another assumption of the coarse-filter/fine-filter approach is that the dynamics of future environments will be similar grosso modo to those of past environments. The approach is thus static and therefore does not provide a means of adapting to future changing environmental conditions. Accordingly, the main criticism of this approach is that because of rapid global change, knowledge of past ecosystem conditions cannot serve to guide forest restoration under future conditions, conditions that entail the development of novel ecosystems (Hobbs et al., 2011; Keane et al., 2009; McDowell et al., 2020). On the other hand, we may assume that native species are adapted to past ecological conditions, and knowledge of species habitat requirements can guide restoration even when future conditions differ from those of the past (Keane et al., 2009).

17.3.2 Natural Disturbance Emulation

Natural disturbance emulation (NDE) has become an important concept when aiming to implement the coarse-filter approach in forest ecosystem restoration and management (Angelstam, 1998; Bergeron et al., 2002; Berglund & Kuuluvainen, 2021; Kuuluvainen, 2009; Stockdale et al., 2016). Essentially, NDE is a strategy to implement the coarse filter over time. Thus, the coarse-filter concept emphasizes maintaining natural broad-scale habitat structures, whereas NDE focuses on the disturbance and successional processes and how to emulate them in forest restoration and management over time. NDE recognizes disturbance dynamics as a critical driver in forest dynamics and biodiversity maintenance (Kuuluvainen & Grenfell, 2012). According to this approach, management actions, especially timber harvesting, are planned to emulate the structural outcomes of natural disturbances typical of the forest landscape to be managed. Special attention is paid to the outcomes of such management at multiple scales, from deadwood microsites to landscape patterns, to provide natural habitat variability for various organisms.

Applying the NDE paradigm to forest restoration and management requires an adequate understanding of the past natural and potential future range of variation in forest structure and dynamics. Thus, it is possible to consider changes in forest disturbance dynamics likely to take place in the future (Cyr et al., 2009). In this manner, the ongoing rapid shifts in forest dynamics because of global stressors and climate warming, increasing disturbances, and land-use changes can be, in principle, incorporated into this approach. Moreover, natural disturbance can promote resilience by enhancing biodiversity and the ability of the ecosystems to resist or recover when hit by perturbations (Drever et al., 2006).

17.3.3 Complex Systems Framework

Traditionally, the boreal forest has been considered a simple system with few tree species and slow, predictable development. The complex systems approach challenges this view (Burton, 2013; Levin, 2005). Any single stand of boreal forest in Fennoscandia is estimated to contain some 2,500 to 5,000 species, with a large number of complex trophic and nontrophic interactions (Kuuluvainen & Siitonen, 2013). Thus, contrary to earlier perceptions, the boreal forest ecosystem holds a web of highly complex interactions (Burton, 2013), which in turn interact with the dynamic physical systems, such as climate and forest management. The boreal forest is, in essence, a complex system, and the goal should be to respect and restore this complexity (Drever et al., 2006; Filotas et al., 2014; Levin, 1998). This calls for a systems approach to the understanding, managing, and restoring of communities of trees and other plants, animals, and microorganisms that interact with their physical environment.

The ecological complexity perspective yields several implications for forest restoration and ecosystem management. First, a holistic approach is compulsory because of the complexity of the system. In landscape restoration, for example, it is necessary to pay attention to the cross-scale interactions of spatial and temporal heterogeneity. Second, the applied conceptual models, e.g., NRV and NDE, and the available reference ecosystems must be adequate to address ecologically important details and variations in the ecosystem (Berglund & Kuuluvainen, 2021). Overly simplistic conceptual approaches, such as conventional even-aged stand management, easily overlook critical details and interactions at spatial scales higher (landscape patterns) and lower (within-stand structures, microhabitats) than that of a tree stand (Kuuluvainen, 2009). Thus, management must address important structures and processes at multiple scales, from decaying logs to landscape patterns of habitats (Puettmann, 2014). Third, forest ecosystems are always undergoing change, and they must be managed by considering their long-term dynamics in a warming climate (Gauthier et al., 2015). Biodiversity and resilience are ultimately based on the adaptive cycle of disturbances and succession. Forests are indeed complex systems, and the challenge is to assimilate this complexity into forest ecosystem restoration and management (Messier et al., 2013).

17.4 When Are Different Strategies Applicable?

The applicability of specific restoration strategies and approaches is always sensitive to location and context (Fig. 17.2). Important issues are, first, how well the natural range of variability (NRV) and disturbance regime are known, and can we expect them to prevail as such in the future, or will they change (even radically), for example, because of climate change. Second, it is important to know the degree to which the restoration process is controllable. The lack of controllability may be because of a poor understanding of intrinsic system dynamics, e.g., in the case of novel ecosystems, or a shortage of managerial resources to carry out monitoring and control measures when needed.

In an ideal situation, NRV is well known and restoration is well controlled; then, it is possible to define specific targets and implement measures to obtain them (Fig. 17.2). Such a situation can be exemplified by developed countries like Sweden and Finland, which have both the research knowledge of reference systems and the resources to carry out and control the restoration process (Kuuluvainen & Siitonen, 2013).

If the controllability of restoration processes is high, but NRV is poorly understood, it becomes possible to apply a passive restoration based on ecosystem self-organization, or a coarse-filter/fine-filter approach based on a general knowledge of NRV (Clewell & McDonald, 2009). Such a situation can be typical in southern boreal forests, where reference systems are lacking because forests have been used for various purposes for hundreds (even thousands) of years. Finally, when the controllability of the restoration process is low, an adaptive management approach is preferable irrespective of the level of local knowledge of NRV. If the level is high, then NDE is applicable, and if the level is low, the robust coarse- and fine-filter approach can be used (Fig. 17.2). Restoration also needs to employ self-organization and be prepared for surprises and the emergence of novel species communities (Hobbs et al., 2011).

At large scales, the goal of restoration is typically to achieve a favorable conservation status for native ecosystem types—including the range of stages of forest succession—and their species assemblages over time. The measures to attain this goal depend not only on the properties of the area to be restored but also on the quality of the surrounding area (the forest matrix) (Fig. 17.3). This highlights that no restoration occurs in isolation and that a favorable conservation status can be

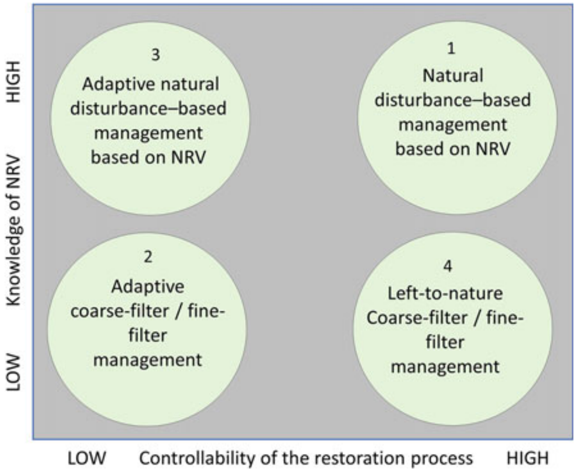

Fig. 17.2 Illustration of different forest restoration strategies in relation to the controllability of the restoration process and the level of understanding of the natural or historical range of variation (NRV). *1* When knowledge of NRV and controllability are both high, natural disturbance emulation is feasible. *2* When both the knowledge of NRV and controllability are low, it remains possible to practice adaptive coarse-filter/fine-filter management by applying a general understanding of NRV features. *3* Situations where knowledge of NRV is high but controllability is low favors use of an adaptive management approach to natural disturbance emulation. *4* A situation of low knowledge of NRV but high controllability allows applying a coarse-filter/fine-filter approach based on general understanding of NRV within similar systems. Modified from Allen et al. (2011) with permission from Elsevier

attained through different combinations of the managed matrix and core protected habitat, depending on their ecological quality. For example, if the forest matrix is under intensive plantation-type management and its habitat quality is low and does not provide habitat for native species, more pressure is put on restoring the full range of habitat and ecosystem types in the restored area (Fig. 17.3; Berglund & Kuuluvainen, 2021). On the other hand, if the matrix is managed on the basis of *ecological forestry* principles (Franklin et al., 2018), less intensive restoration may be required to obtain a favorable conservation status.

17.5 Adaptive Cycle and Adaptive Capacity: A Comprehensive Restoration Framework Under Climate Change Conditions

The adaptive cycle provides a universal metaphor and framework for describing and understanding long-term dynamics and change in complex socioecological systems (Fig. 17.4; Gunderson & Holling, 2001). The adaptive cycle is thought to be central

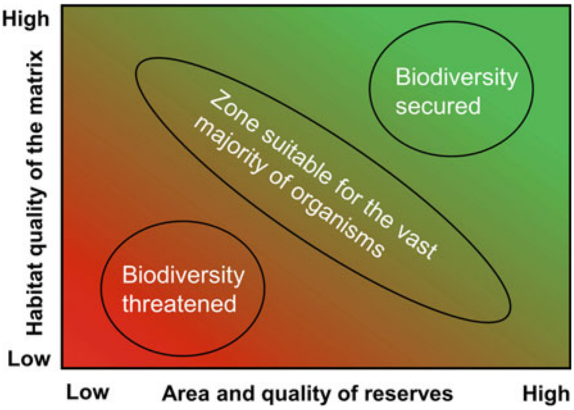

Fig. 17.3 Attaining the favorable conservation goals in restoration requires a landscape- or region-wide approach that includes both the area to be restored and the surrounding managed forest *matrix*. The level of biodiversity conservation can range from secured (*green*) to poorly secured or threatened (*red*). A reasonably favorable conservation status (*green–red transition*) can be achieved through various combinations of restored core area and ecosystem-based management of the surrounding managed landscape matrix. Modified by permission of Island Press, Washington, DC from Lindenmayer and Franklin (2002) *Conserving Forest Biodiversity*. Copyright © 2002 by the authors

to the endogenous processes of self-organization and evolution of complex systems through time (Levin, 1998, 2005). The widespread distribution of the adaptive cycle in ecosystem dynamics has been confirmed in many studies (Sundstrom & Allen, 2019). Thus, the adaptive cycle is useful as a conceptual model for management and restoration purposes, as it simplifies highly complex system behavior into four ubiquitous phases in ecosystem dynamics: (1) growth and development, (2) conservation, (3) release, and (4) reorganization. Most importantly, the adaptive cycle explains how ecosystems adapt to changing environmental conditions at multiple scales, a property necessary during periods of climate change. We suggest that the adaptive cycle and its extension, the nested adaptive cycle (*panarchy*), provide a comprehensive strategic ecological and evolutionary framework for forest ecosystem restoration (Fig. 17.4; Gunderson & Holling, 2001).

For forest restoration to be successful over the long term, a holistic approach is necessary where all four stages of the adaptive cycle and their dynamics are considered in relation to each other (Fig. 17.4; Box 17.1). This holistic approach stresses managing and restoring the naturally occurring processes and dynamics in the landscape. Forests are therefore allowed to complete full disturbance–succession cycles, from post-disturbance conditions to old-growth forest (Fig. 17.4). A landscape can also host multiple types of cycles depending on disturbance type. An example is provided by beaver pond dynamics, which can interact with and be embedded in the forest disturbance cycle (Box 17.2; Kivinen et al., 2020; Nummi & Kuuluvainen, 2013).

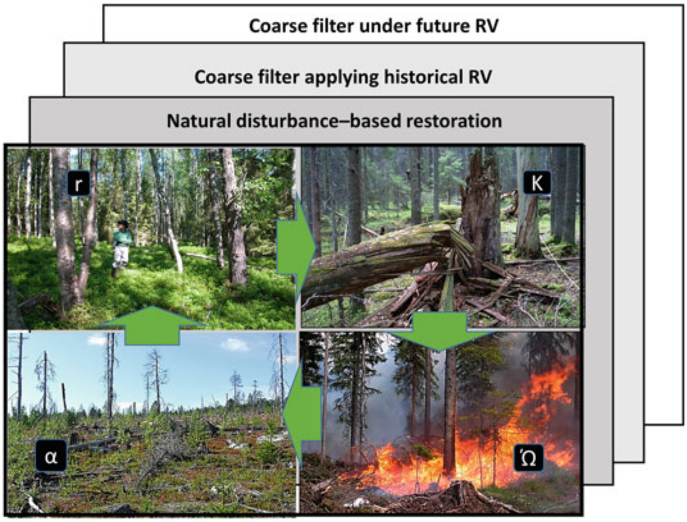

Fig. 17.4 Illustration of a typical adaptive cycle in the boreal forest with four stages: release, fire (Ω), reorganization (α), exploitation (r), and conservation (K). Such adaptive disturbance–succession cycles create the dynamic NRV that enables the adaptation of the ecosystem to changing environmental conditions. To become a useful strategic model in restoration and sustainable management, this conceptual model needs to be translated into a quantitative model based on knowledge of NRV, including the emulation of the natural disturbance regime. *Photo credits* Timo Kuuluvainen

Box 17.1: The Four Stages of the Adaptive Cycle (Gunderson & Holling, 2001)

Release, Ω Periodic disturbances are necessary to maintain habitat variation and biodiversity. Disturbances are also essential for the adaptive cycle, as they release growth resources and space and create critical post-disturbance structures, such as abundant deadwood and complex stand structures (Johnstone et al., 2016). The natural disturbance emulation approach is based on these notions and provides methods of implementing disturbance into forest restoration. The key NRV properties are the type, severity, size, and frequency of disturbances.

Reorganization, α This is a crucial stage of ecosystem dynamics promoting the adaptive capacity of the ecosystem to be restored. Here the critical process is the post-disturbance reassembly of the ecological community, as determined by the introduction or availability of new species and genotype assemblages, which through competition form novel communities potentially better adjusted to changing environmental conditions. This facilitates the system's adaptation to novel conditions, such as a warming and drying climate (Gauthier et al., 2015).

***Exploitation*, r** This part of ecosystem dynamics is perhaps most often addressed in restoring damaged or degraded ecosystems, as it represents the early-successional phase. Important natural processes in the adaptive cycle of ecosystems are the self-organization of species assemblages—through space filling and competitive self-thinning through multiple successional pathways—and the longevity of the successional processes at the landscape scale.

***Conservation*, K** This refers to the mature and late-successional phase where growth resources are tied to standing biomass, and changes in vegetation structure are slight and take place at a small scale. Here, the traditional example is old-growth forests and their restoration and conservation. Important NRV variables are the variation of old-growth types, their structure, and the areal proportions of old-growth forest in the past and present.

The adaptive cycle is closely related to and feeds on biodiversity (Fig. 17.5). The two main interrelated restoration goals are maintaining native biodiversity and keeping the adaptive cycle in operation to provide a continuity of habitats through disturbance and succession (Fig. 17.4). If successful, both goals will contribute to forest resilience and adaptive capacity. Resilience here means an ecosystem's resistance to disturbance (short-term) or its ability to recover when perturbed (medium-term). Adaptive capacity denotes the ecosystem's (long-term) evolutionary adaptive potential (Sgrò et al., 2011).

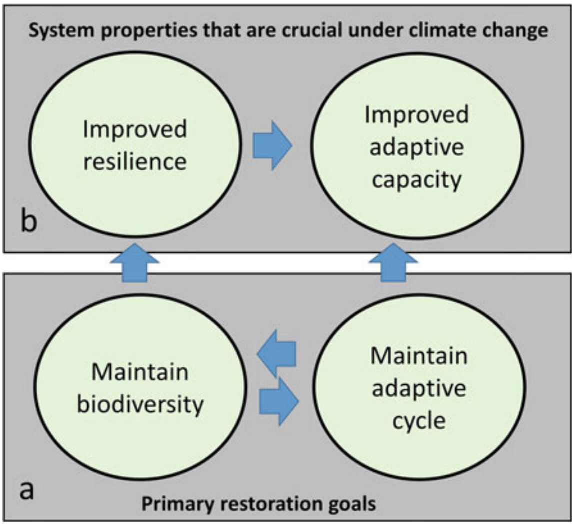

Fig. 17.5 Illustration of the relationships of key strategic concepts of ecological restoration; **a** the primary restoration goals maintain biodiversity by ensuring diverse habitats through the adaptive disturbance–succession cycle (see Fig. 17.4); **b** if successful, the goals improve forest resilience and adaptive capacity, properties that are crucial under conditions of rapid climate change

17.6 Strategic Questions: What, How Much, and When to Restore?

In practice, ecosystem types are often defined as comprehensive vegetation communities, or habitat types, which are used as proxies to represent natural ecosystems and their dynamics (Landres et al., 1999). The goal of restoration is the recovery of a favorable conservation status of all native ecosystem types and their natural dynamic stages in terms of the adaptive cycle (Fig. 17.4). At a large scale, this requires answers to three strategic questions: (1) What to restore? (2) How much to restore? (3) When to restore? The operational question, How to restore? must also be answered; however, most texts on restoration focus on this last question, and, from a policy and planning point of view, the three first questions are more important.

(1) What to Restore? This is a strategic question, as we can focus on restoring, for example, species, populations, communities, habitats, or full ecosystems at different scales. This chapter deals with forest ecosystem restoration, which requires an understanding of the ecosystem types and their intrinsic dynamics over time, as defined by the four stages of the adaptive ecosystem cycle (Fig. 17.4). This requires a classification of the ecosystem types to be restored (Fig. 17.6; Berglund & Kuuluvainen, 2021). Such a classification of forest ecosystem types could be based, for example, on soil fertility and moisture, tree species composition, disturbance origin, and successional stage, or a combination of these. The classification of ecosystem types should capture the essential features of NRV but also restrict the number of classes to allow their application in practical restoration (Fig. 17.6).

It should also be understood that some ecosystem types and dynamics may have completely disappeared; the question then is whether their restoration is possible and reasonable (Jackson & Hobbs, 2009). An example is provided by the most fertile herb-rich forest sites, which have been transformed into agricultural fields across most of Europe. Another interesting case is beaver-modified habitats in boreal forest landscapes (Box 17.2).

(2) How Much to Restore? This question urges managers to define how much should be done to achieve a favorable conservation status of native ecosystem types (Fig. 17.6). Answering this question requires estimating the natural or historical proportions of ecosystem types (NRV) and comparing them with their current extent (Angelstam & Andersson, 2001; Berglund & Kuuluvainen, 2021). This approach allows the quantification of shortcomings in the representativeness of different ecosystem types and their dynamic stages (gap analysis; Berglund & Kuuluvainen, 2021). However, setting quantitative targets for the representativeness and dynamics of ecosystem types over time—to secure a favorable conservation status—is a tricky question (Bengtsson et al., 2003).

To answer the question, How much to restore? typical values derived from ecological theory have referred to, for example, 20%–50% of original habitat cover (Angelstam & Andersson, 2001; Berglund & Kuuluvainen, 2021; Fahrig, 2001; Hanski, 2011; Wilson, 2016). Naturally, the issue is more complicated, including questions

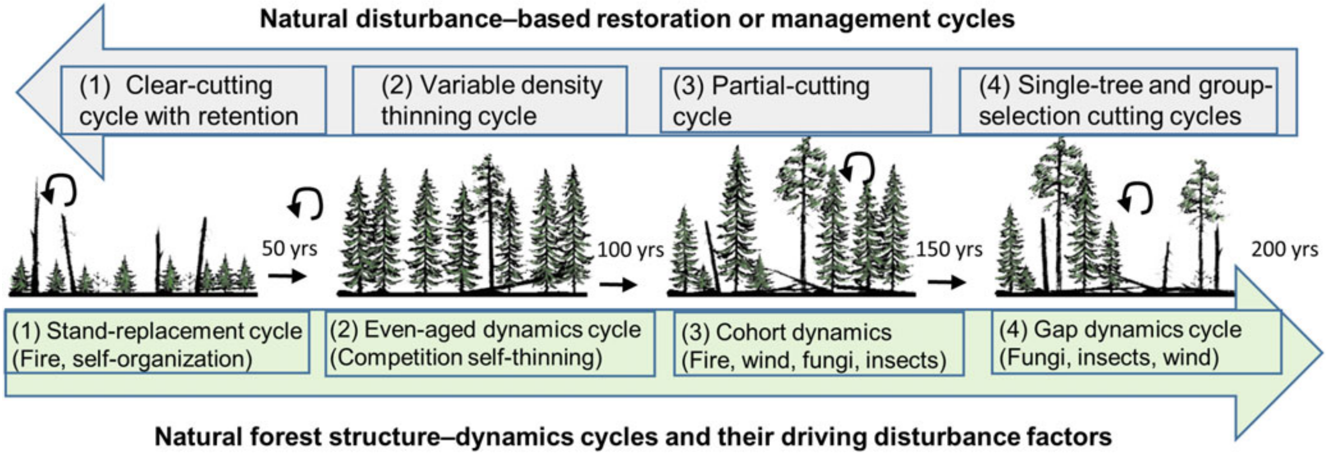

Fig. 17.6 The adaptive cycles in forest ecosystems are expressed as variable disturbance-driven forms that must be accounted for in restoration. An example of a strategic answer to the question, What to restore? is to divide the NRV of forest structure into four types of structure–dynamics cycles (*green arrow*) identified by their main driving disturbance factors. Embedded in the *1* stand-replacing fire-driven "large cycle" are three "small cycle" structure–dynamics cycles: *2* even-aged, *3* cohort, and *4* gap-dynamics cycles, with their respective restoration or management cutting cycles to be applied (*gray arrow*). The answer to, How much to restore? for each type of structure–dynamics cycle depends on their historical proportions, informed by the knowledge of the NRV of the associated disturbance regime. The answer to, When to restore? depends on the current state and proportions of habitats compared with the natural state and the disturbance return intervals

involving spatial and size distributions, temporal dynamics, and connectivity, all of which affect the conservation function of the habitat network (Angelstam et al., 2020; Ward et al., 2020). For example, restoring the *growth* phase (Fig. 17.4) requires information about the variation in successional pathways and their longevity and stand self-organization, as determined by the reference disturbance regime (Fig. 17.6; Kuuluvainen, 2009).

(3) When to Restore? Securing the Adaptive Cycle The question, when to restore? refers to the need to secure the continuity of key ecological processes and functioning of the adaptive cycle (Fig. 17.4). This can be realized by emulating the structure–dynamics cycles in management (Fig. 17.6). In some situations, the adaptive cycle can be restored and maintained without intervention. This could be the case, for example, in old humid spruce forests where autogenic disturbances and small-scale gap dynamics are driving the adaptive cycle. On the other hand, if an important natural disturbance driver such as fire is suppressed, it may be necessary to use fire as a restoration tool or at least emulate fire impacts in restoration cuttings to maintain the natural-like habitat distribution and the functioning of the adaptive cycle over time (Berglund & Kuuluvainen, 2021; Vanha-Majamaa et al., 2007).

To answer the three strategic questions discussed above, one can use strategic models to plan how to maintain favorable habitat status and dynamics through space and time (Fig. 17.6; Kuuluvainen & Grenfell, 2012). However, only a few specific strategic models have been proposed to transform strategic restoration principles into practical management solutions that also consider the adaptive cycle. These models include the multicohort model (Bergeron et al., 2002), the ASIO model (Angelstam, 1998) discussed in Kuuluvainen and Grenfell (2012) and Kuuluvainen (2017), and the revised-ASIO model proposed by Berglund and Kuuluvainen (2021).

(4) How to Restore? This operational question is most commonly addressed in restoration, which is a practical undertaking, and it is dealt with in many papers and textbooks (e.g., Allison & Murphy, 2017; Halme et al., 2013). Because the focus of this chapter is on strategic choices, we do not go into detail here. Some practical and tactical methods are described elsewhere (Kuuluvainen, 2017). However, the key issues are to strive for representativeness and favorable conservation status of the various phases of the adaptive cycle in different ecosystem types (Fig. 17.2; Berglund & Kuuluvainen, 2021). For example, if conservation has focused on old-growth forests, there may be a shortage of natural early-successional open-canopied forests that would secure ecological communities adapted to such habitats (Swanson et al., 2011). On the other hand, restoring old-forest habitat features, such as deadwood structures, may be urgent if there is a lack of old-growth forest. What the adaptive cycle framework emphasizes, however, is the restoration of the dynamic continuity of all-natural habitat types to provide ecological and evolutionary resilience provided by the adaptive cycle (Figs. 17.2 and 17.5).

Box 17.2 Beaver: A Keystone Disturbance Agent of Boreal Landscapes

In the boreal forest, beavers (*Castor canadensis* and *C. fiber*) provide an example of a keystone ecosystem modifier (Johnston, 2017) extirpated from many parts of the boreal zone because of heavy exploitation for the animal's fur. Beavers are now returning to many parts of their original range in Eurasia and North America (Halley et al., 2021; Whitfield et al., 2015). This renewal provides a possibility of restoring former beaver habitats and their dynamics at landscape scales. Some beaver-affected areas may comprise up to 26% of the landscape (Naiman et al., 1988); in the boreal region, however, it is normally much less, e.g., 2.8% (Parker et al., 1999).

The power of ecological engineering by beavers is based on their ability to build dams (Johnston, 2017). The damming of creeks and ponds creates wetland habitats and successional pathways that otherwise would not exist in many boreal landscapes (Feldman et al., 2020). The beaver is unique in terms of its role in flooding riparian forests and transforming terrestrial habitats into aquatic ones. When beavers abandon a pond and the dam collapses, the terrestrial habitat returns. For both events, an early-successional stage is created.

Within a boreal forest matrix, beaver flooding can be viewed as a patch disturbance (Johnston & Naiman, 1990; Nummi & Kuuluvainen, 2013; Remillard et al., 1987). Whereas disturbances such as fire and windstorms mainly strike upland forests, beavers most pronouncedly affect lowland riparian stands. Fires and storms are very stochastic events, having local return times of tens to hundreds of years. In contrast, beaver disturbance in an active beaver landscape is more predictable, both spatially and temporally (Nummi & Kuuluvainen, 2013).

Kivinen et al. (2020) recently studied the effect of beavers on landscape heterogeneity in Finland using data of the yearly occupancies of beavers in a landscape over half a century. During this time, beavers colonized the landscape, and the number of beaver sites increased from 6 to 69. What is noteworthy in this boreal setting, however, is that at certain points, the amount of flooded land was much less than observed in more temperate areas (Naiman et al., 1988). Rather, the cumulative number of beaver-affected sites increased steadily. Along with this increase, different processes occurred, affecting the distribution and properties of the riparian habitats (Kivinen et al., 2020). First, the distance between beaver sites declined, and *hot spots* of spatially clustered beaver sites were then formed (Kivinen et al., 2020).

The biodiversity-enhancing impact of beavers relates to how they facilitate the establishment of numerous organisms (Stringer & Gaywood, 2016). Various species and species groups benefit from the different successional stages associated with beaver sites; these taxa benefiting from flooding phases include invertebrates (Bush et al., 2019; Nummi et al., 2021), frogs (Dalbeck et al., 2007), and water birds (Nummi & Holopainen, 2014). In the terrestrial system, beaver-affected processes include the riparian forest becoming more dominated by deciduous trees after flooding (Hyvönen & Nummi, 2008). This shift in vegetation is notable because herbivores normally push forests toward a more coniferous direction because of the foraging preference of herbivores on deciduous trees. Greater amounts of deciduous trees benefit animals such as moose (Nummi et al., 2019) but also beaver itself when it reoccupies sites (Labrecque-Foy et al., 2020). Beaver flooding also creates deadwood (Thompson et al., 2016). Beaver sites may contain different-sized deadwood resulting from consecutive floods (Kivinen et al., 2020), and the presence of beavers in the landscape results in spatiotemporal deadwood continuity (Thompson et al., 2016).

17.7 Conclusions

The rapid loss of global forest area and degradation of forest ecological conditions because of global change (Gauthier et al., 2015; McDowell et al., 2020) have evoked an urgent need to develop and apply ecologically sound restoration and sustainable management approaches that can be applied to various situations and scaled over large areas (Angelstam et al., 2020; Berglund & Kuuluvainen, 2021; Kuuluvainen, 2017). Over time, different approaches to conservation and restoration have been proposed, reflecting the increasing understanding of forest ecosystems and their intrinsic structure and dynamics (Fig. 17.1).

Forest restoration strategies and tactics should be based on an ecological and evolutionary understanding of long-term ecosystem structure and dynamics (Rice & Emery, 2003; Sgrò et al., 2011), as the species, communities, and ecosystems being restored have emerged via evolutionary processes operating under past environmental conditions. The assembly of species and communities in ecosystems is by and large regulated by properties of the prevailing disturbance–succession cycles and the resulting habitat mosaic structure at multiple scales (Johnstone et al., 2016). Therefore, a holistic understanding of ecosystem structure and function at multiple scales is necessary to set tangible restoration targets and effective actions.

In a time of climate change, the adaptive capacity of ecosystems should become the fundamental strategic priority and guiding principle of ecological restoration. This requires viewing and understanding forests as complex adaptive systems where the most important long-term goal is to restore and maintain the favorable conservation status of habitat types and the native adaptive cycles driven by the cyclic dynamics of forest disturbance and succession (Fig. 17.4).

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