Title

Searching for resilience: addressing the impacts of changing disturbance regimes on forest ecosystem services.

Journal
Journal of Applied Ecology, 53(1)

ISSN
0021-8901

Authors

Seidl, Rupert
Spies, Thomas
Peterson, David
et al.

Publication Date
2016-02-01

DOI
10.1111/1365-2664.12511

Peer reviewed

J Appl Ecol. Author manuscript; available in PMC 2017 February 01.

Published in final edited form as:
J Appl Ecol. 2016 February 1; 53(1): 120–129. doi:10.1111/1365-2664.12511.

Searching for resilience: addressing the impacts of changing disturbance regimes on forest ecosystem services

Rupert Seidl[1,*], **Thomas A. Spies**[2], **David L. Peterson**[3], **Scott L. Stephens**[4], and **Jeffrey A. Hicke**[5]

[1]Institute of Silviculture, Department of Forest- and Soil Sciences, University of Natural Resources and Life Sciences (BOKU), Peter Jordan Straße 82, 1190 Wien, Austria

[2]USDA Forest Service, Pacific Northwest Research Station, Corvallis, OR 97331, USA

[3]USDA Forest Service, Pacific Northwest Research Station, Seattle, WA 98103, USA

[4]Ecosystem Sciences Division, Department of Environmental Science, Policy, and Management, University of California, Berkeley, CA 94720, USA

[5]Department of Geography, University of Idaho, Moscow, ID 83844, USA

Summary

1. The provisioning of ecosystem services to society is increasingly under pressure from global change. Changing disturbance regimes are of particular concern in this context due to their high potential impact on ecosystem structure, function and composition. Resilience-based stewardship is advocated to address these changes in ecosystem management, but its operational implementation has remained challenging.

2. We review observed and expected changes in disturbance regimes and their potential impacts on provisioning, regulating, cultural and supporting ecosystem services, concentrating on temperate and boreal forests. Subsequently, we focus on resilience as a powerful concept to quantify and address these changes and their impacts, and present an approach towards its operational application using established methods from disturbance ecology.

3. We suggest using the range of variability concept – characterizing and bounding the long-term behaviour of ecosystems – to locate and delineate the basins of attraction of a system. System recovery in relation to its range of variability can be used to measure resilience of ecosystems, allowing inferences on both engineering resilience (recovery rate) and monitoring for regime shifts (directionality of recovery trajectory).

4. It is important to consider the dynamic nature of these properties in ecosystem analysis and management decision-making, as both disturbance processes and mechanisms of resilience will be subject to changes in the future. Furthermore, because ecosystem services are at the interface between natural and human systems, the social dimension of resilience (social adaptive capacity

---

[*]Correspondence author. rupert.seidl@boku.ac.at.

Data accessibility
Data have not been archived because this article does not contain data.

and range of variability) requires consideration in responding to changing disturbance regimes in forests.

5. *Synthesis and applications*. Based on examples from temperate and boreal forests we synthesize principles and pathways for fostering resilience to changing disturbance regimes in ecosystem management. We conclude that future work should focus on testing and implementing these pathways in different contexts to make ecosystem services provisioning more robust to changing disturbance regimes and advance our understanding of how to cope with change and uncertainty in ecosystem management.

Keywords

climate change impacts; ecological resilience; ecosystem services; engineering resilience; forest ecosystem management; natural disturbance; range of variability; socio-ecological resilience

Introduction

Ecosystems contribute to human well-being by providing a wide range of ecosystem services to society (MA 2005). As ecosystems are subjected to mounting pressure from global change, their functions and services are at risk or declining (Carpenter *et al.* 2009), while societal demands for goods and services increase. A major challenge for current ecosystem management is to sustain the provisioning of ecosystem services in a rapidly changing world.

A primary concern is the growing mismatch in temporal scales between anthropogenic alterations of the environment and ecological mechanisms of adaptation. The high rate of global change makes it increasingly difficult for the biotic world to adapt (Burrows *et al.* 2011), especially in forest ecosystems characterized by long-lived, immobile vascular plants. Profound changes in the climate system are expected to unfold within one tree generation or less. This rate of change may exceed the capacity of many species to adapt through processes such as regeneration, range shifts and genetic change (but see Hamrick 2004) and increases the potential for disruptive changes in biological systems.

Natural disturbances cause abrupt changes in forests with a lasting effect on forest dynamics and succession over decades to centuries (Carpenter & Turner 2001). Disturbance by, for example, wildfire, bark beetles or windstorms causes pulses of tree mortality, disrupts ecosystem structure, community or population, and changes resource availability in the biophysical environment (Turner 2010). Forest species are well adapted to and have co-evolved with disturbance regimes (Gutschick & BassiriRad 2003). However, disturbance regimes are changing as a result of global change (Westerling *et al.* 2006; Seidl *et al.* 2014), and implications of these changes for forests and the services they provide to society are uncertain.

Considering the rate of environmental changes relative to time-scales of natural adaptation in forest ecosystems and long lead times associated with forest management, responses to ongoing changes require timely implementation. One such response strategy prominently discussed in the recent literature is to foster resilience (Biggs *et al.* 2012). Resilience has been defined in many ways (Brand & Jax 2007) including engineering resilience (recovery to a previous state), ecological resilience (remaining within the prevailing system domain through maintaining important ecosystem processes and functions or shifting to an alternative ecological domain) and socio-ecological resilience (the capacity to reorganize and adapt through multi-scale interactions between social and ecological components of the system) (Carpenter *et al.* 2001; Holling & Gunderson 2002). Here, we address all levels of resilience which have relevance at different spatiotemporal and administrative levels of ecosystem management. Promoting resilience through management is especially relevant in the context of changing disturbance regimes, because increasing resistance to disturbance and reducing risk are limited by the uncertainty and stochasticity of disturbance processes (Seidl 2014). Implementing resilience concepts in forest management is challenging because it is difficult to define indicators of resilience, mismatches in scale exist among social, management and ecological processes, and knowledge gaps remain about underlying processes (Puettmann, Coates & Messier 2009; Reyer *et al.* 2015).

In response, we (i) highlight why a focus on resilience towards changing natural disturbance regimes is needed in forest ecosystem management; (ii) present an operational description of resilience in the context of disturbance management, and (iii) discuss how to foster resilience of forest ecosystem services in changing disturbance regimes. To address the first objective, we follow the questions suggested by Carpenter *et al.* (2001) – resilience of what, to what – and review recent and expected future changes in disturbance regimes and their effects on forest ecosystem services. Subsequently, to aid applied ecologists, we operationalize resilience by describing how theoretical concepts of ‘resilience thinking’ link to established approaches of disturbance ecology and adaptive ecosystem management. Finally, addressing the current need of forest ecosystem managers, we present principles and pathways for fostering resilience in ecosystem management, detailing how changing disturbance regimes can be tackled in management. We draw on experiences with disturbance from wind, bark beetles and wildfire in temperate and boreal forest ecosystems [see Allen *et al.* (2014) and Nash *et al.* (2014) for information on other ecosystems].

Resilience to what: changing forest disturbance regimes

OBSERVED CLIMATE-RELATED CHANGES IN DISTURBANCE REGIMES

Forest disturbance regimes are highly sensitive to climate (Dale *et al.* 2001; Turner 2010). Consequently, the ongoing changes in the global climate system have already altered disturbance regimes in some ecosystems. For example, insect outbreaks have spread to higher latitudes and altitudes as a result of reduced thermal constraints by warming temperatures (Weed, Ayres & Hicke 2013). The positive influence of warming on insect population dynamics – increasing reproductive rate and reducing winter mortality – has led to increasing damage in some forest ecosystems (Seidl *et al.* 2014; Creeden, Hicke & Buotte 2014). Concurrently, climatic extremes such as longer and more intensive droughts are increasing the susceptibility of trees to insect attacks via exhaustion of non-structural carbohydrate reserves, weakening secondary defence reactions to bark beetles (Bentz *et al.* 2010).

Water deficit and temperature are also important constituents of fire weather, and the observed increases in fire weather severity are linked to changes in these climate variables (Aldersley, Murray & Cornell 2011). As a result, fire probability and area burned have already increased in some forest ecosystems (see Soja *et al.* (2007) for an analysis of boreal forests). The fire season has lengthened due to earlier snowmelt and a prolonged period capable of propagating fire, for instance in the western USA since the mid-1980s (Westerling *et al.* 2006). Furthermore, climate change is likely also linked to recently observed 'mega-fires' (Stephens *et al.* 2014), *inter alia* through an increased propensity for and severity of climatic extremes.

While a strong link exists between global warming, drought severity and heat waves (IPCC 2012), possible changes in extreme events such as windstorms are still under debate. Trends in cyclonic storms in Europe and hurricanes in eastern North America are still inconclusive (e.g. Knutson *et al.* 2010), although links have been suggested for some trends in storms. Nonetheless, climatic changes have contributed to observed increases in wind disturbance in Europe by reducing tree soil anchorage by decreasing winter soil frost (Usbeck *et al.* 2010).

OTHER CAUSES OF RECENT DISTURBANCE CHANGE

Beyond climatic change, changes in land use and forest management, driven by global economic and social forces, can also affect disturbance regimes. For example, management-mediated alterations of forest structure and composition were important factors contributing to the observed increase in wind disturbance in Europe (Seidl, Schelhaas & Lexer 2011), and changes in land use have affected fire regimes of the Mediterranean basin (Pausas & Fernández-Muñoz 2012). Furthermore, fire suppression policies in the 20th century have led to increasing fuel loads in many US forests (Stephens *et al.* 2013). These policies have facilitated a shift from fire-adapted (and typically light-demanding) tree species to shade-tolerant species (Merschel, Spies & Heyerdahl 2014), which are generally more susceptible to fire and drought, and increase the risk of crown fires in dense, vertically structured canopies.

Likewise, the recently observed bark beetle outbreaks in North America and Europe are not solely a result of climate change, but also relate to forest structure that is prone to such disturbances (i.e. well-connected landscapes of mature host trees for bark beetles; Hicke & Jenkins 2008). Furthermore, a focus on commercially valuable conifer species in management has additionally increased the susceptibility to bark beetles in areas such as Central Europe (Seidl, Schelhaas & Lexer 2011). Observed trends in disturbance frequency and severity are thus driven by combined effects of past management, climatic variation (e.g. Pacific Decadal Oscillation) and climate change. Therefore, a long-term perspective is needed to detect changes in forest disturbance regimes, and landscape patterns and processes as well as the local context need to be considered in their attribution (Littell *et al.* 2009).

POTENTIAL FUTURE CHANGES IN FOREST DISTURBANCE REGIMES

The climatic influences on disturbances described above are likely to continue in the coming decades. Fire weather will become more severe around the globe (Flannigan *et al.* 2013), and insect population dynamics will be further affected by continuing climate change (Bentz *et* *al.* 2010). This could lead to situations in which large disturbance events of the past, like the Yellowstone Fire of 1988, could become the new norm in the future (Westerling *et al.* 2011). For Europe, it has been estimated that what was statistically a once-in-32-years bark beetle damage level between 1971 and 2001 could be reached every other year in 2021–2030 (Seidl *et al.* 2014). However, the complexities and interactions between climate, forest and disturbance are not fully considered in most projections of future disturbance change, which contributes to remaining uncertainties on future disturbance regimes. It has, for instance, been shown that climate-mediated increases in disturbance will eventually lead to reorganization of the system (e.g. towards species less susceptible to bark beetles, or more adapted to frequent fires), causing a dampening system-level feedback on disturbance regimes (Temperli, Bugmann & Elkin 2013). However, although such feedbacks are an important pathway for forest ecosystems to adjust to changing disturbance regimes, an autonomous reorganization of ecosystems would require many decades to centuries and might not result in a societally desired set of ecosystem services. Therefore, an important task for ecosystem management is to support adaptive pathways of forest ecosystems that are also congruent with social systems.

Resilience of what: ecosystem services provisioning under disturbance

PROVISIONING AND REGULATING ECOSYSTEM SERVICES

Many of the short- to mid-term changes expected in disturbance regimes and long-term reorganizations in their wake will challenge efforts to sustainably and continuously provide ecosystem services. Timber, fibre and fuelwood are important provisioning services. Disturbances interfere with these services in a variety of ways, including the loss of biomass through consumption by fire, the devaluation of timber by wind breakage and fungal infections following bark beetle infestations, and the reduced increment through premature mortality (Gardiner *et al.* 2010). Moreover, both biological aspects and economics of biomass production are negatively affected by disturbance, for example through increased harvesting costs in post-disturbance salvaging and market depressions as a result of disturbance-induced pulses in supply (Prestemon & Holmes 2004).

Freshwater supply, an important provisioning service, can be negatively affected by increasing disturbance. Disturbances can lead to increased soil erosion and to leaching of nitrate, reducing water quality (Mikkelson *et al.* 2013). An important regulating service of forests also related to water is the protection of society and human infrastructure against natural hazards such as flooding and snow avalanches. Disturbances diminish the buffering effect of forests on water runoff and provide reduced long-term protection against the initiation and flow of snow avalanches (Zurbriggen *et al.* 2014).

Although these regulating services are of central importance for human well-being particularly in densely populated mountain areas, forest ecosystems also have a global regulation function regarding the climate system. They are the largest terrestrial carbon (C) storage and buffer climate change through taking up a considerable proportion of anthropogenic CO_2 emissions from the atmosphere. In the wake of a high-severity disturbance event, a large share of the stored C can be rapidly released back to the atmosphere. Climate-mediated increases in disturbances can thus create an amplifying feedback to the global climate system (Kurz *et al.* 2008; Seidl *et al.* 2014).

CULTURAL AND SUPPORTING ECOSYSTEM SERVICES

In addition to provisioning and regulating services, cultural and supporting services are also affected by intensifying disturbance regimes. The recreational value of forest landscapes, for instance, can be strongly diminished by a disturbance event (Sheppard & Picard 2006), as dead trees are frequently perceived as less scenic then live stands and create hazards for tourists. Consequently, recreational sites such as campgrounds and trails are often closed after severe disturbances because of the risk of falling trees. Human health might also be negatively affected by changing forest disturbance regimes (Embrey, Remais & Hess 2012). Furthermore, important supporting services such as soil formation and primary production are interrupted by disturbance. Losses can occur through reduced leaf area and an extended post-disturbance period lacking substantial canopy cover (Peters *et al.* 2013). In summary, all four categories of ecosystem services recognized by the Millennium Ecosystem Assessment (MA 2005) – provisioning, regulating, cultural and supporting services – are predominately negatively affected by increasing disturbance frequencies and severities (Thom & Seidl 2015).

Assessing and quantifying resilience to changing disturbance regimes

RESILIENCE AND ECOSYSTEM MANAGEMENT

Much of natural resource management world-wide has been an effort to control nature in order to harvest its products, reduce its threats and establish predictable outcomes for the short-term benefit of humanity (Holling & Meffe 1996). Socioeconomic goals have driven efforts to completely suppress natural disturbances. A frequent result of such a command-and-control approach is a reduced range of natural variation of ecosystems in an attempt to increase their predictability or stability (Duncan, McComb & Johnson 2010). This commonly results in ‘the pathology of natural resource management’ (Holling & Meffe 1996): when the natural variation is reduced, the system loses resilience. The end result is ecosystems that may become more vulnerable to undesirable change both in fundamental character and in services they provide.

In response, resilience is becoming a guiding principle for ecosystem management, as many ecologists and managers realize that stability and fixed reference conditions are not consistent with functioning of ecosystems, which in turn is the prerequisite for many desired ecosystem services. Resilience per se is not a normative concept because it describes dynamic behaviour regardless of its desirability. Resilience can be positive (e.g. rapid recovery of clean water production in a watershed after a wildfire) or negative (e.g. persistence of an invasive species after disturbance). In most management-related uses, particularly in the context of global change, resilience is mostly associated with a positive or desired outcome. However, in ecosystems that are unresponsive or resistant to efforts to sustain or promote ecosystem services, resilience can be an undesired system property.

KEY DETERMINANTS OF FOREST RESILIENCE TO NATURAL DISTURBANCE REGIMES

Regimes—Resilience in the context of disturbance is best examined through the lens of disturbance regimes. Disturbance regimes are described at large enough spatial and temporal scales for characteristics of disturbances to emerge with distinctive distributions of type, severity, frequency and size (Turner 2010). The concept assumes that characteristic species and ecosystem functions are contingent on the collective behaviours of disturbances. When we talk about resilience to changes in disturbances, it is important to address disturbance regimes and their specific spatiotemporal time frames, rather than focusing on individual disturbance events. The main constituents of disturbance regimes, such as the main disturbance agents of a regime, are generally well known for many landscapes and ecosystems (e.g. Hessburg & Agee 2003; Nagel, Svoboda & Kobal 2014). However, in much fewer cases, it is currently possible to quantify the bounds of their behaviours in terms of ranges and probabilities for a number of disturbance-mediated ecological states and process metrics.

Ecosystem attractors and recovery—Central for characterizing disturbance regimes and their outcomes in terms of ecosystem processes and services is the concept of historical range of variation (HRV), that is the historical envelope of possible ecosystem conditions under the prevailing disturbance regime (Keane *et al.* 2009). In the parlance of the ball-and-cup metaphor of resilience (Carpenter *et al.* 2001; Brand & Jax 2007), the HRV delineates the past basin of attraction of the system (the location and extent of the cup) in phase space (Fig. 1). HRV has been characterized through historical studies (e.g. dendroecology and historical forest inventories) and modelling, but specific details remain difficult to empirically validate because of extended temporal scales and interference of historic land use and management.

Successional and recovery processes are a second important descriptor of ecosystem resilience, as they form the engines of ecosystem responses to disturbances (Fig. 1). In the ball-and-cup metaphor of resilience, they represent the strength of the attractor, or the slope of the cup. However, succession and recovery are controlled by a large number of factors including species life histories, community interactions, soil, climate and disturbance legacies, and are considerably more complex than a simple return to equilibrium. In fact, multiple pathways of succession and recovery exist in many systems, where ecological responses to disturbance events do not always proceed along the same pathway, and ‘endpoints’ of succession are not necessarily the same (especially at fine scales) over a series of disturbance and recovery cycles (Tepley, Swanson & Spies 2013).

As proposed by the panarchy model of nested adaptive cycles (Holling & Gunderson 2002; Allen *et al.* 2014), such complexities result from variations in the interplay between the stabilizing effect induced by large-scale system memory and a cascading effect of destructive disturbances from lower to higher system levels. This complex interplay across scales is one reason why high-resolution landscape-scale approaches are required to describe and evaluate attractors and recovery in the context of forest resilience, addressing scales above and below the focal scale of management (i.e. the stand scale).

Social dimension—The resilience of ecosystem services provision is determined not only by ecological processes and dynamics but also by social dimensions. Of central importance is the adaptive capacity of societies with regard to (disturbance-related) changes in ecosystem services provisioning. In some instances, the social system might be able to buffer or adapt to climate-mediated changes in ecosystems, and thus maintain human well-being. In the context of provisioning services such as timber production, a disturbance-related change in the provisioning of large diameter timber could, for instance, be substituted by a shift to engineered wood products (e.g. composite lumber) based on smaller diameter trees. However, maintaining ecosystem services through societal adaptation can come at a considerable cost (e.g. resulting from the required changes in the wood-processing industry in the abovementioned example). Furthermore, such adaptive behaviour is generally easier to implement for *ex situ* ecosystem services (i.e. consumed outside of the landscape from which they are supplied) compared to *in situ* ecosystem services (i.e. where supply and demand are not spatially disparate). Altered disturbance regimes have the potential to diminish locally important regulating services and might require technical measures such as dams and avalanche barriers to protect humans and infrastructure. This is an example in which a change in ecosystem service supply is compensated through an engineering solution, which might be considerably more expensive and could have other negative side effects. Because ecosystems frequently provide more than a single ecosystem service to society, trade-offs need to be considered in both assessment and response to changing disturbance regimes.

CHANGING DISTURBANCE REGIMES AND RESILIENCE PROPERTIES

Using its above-described constituents, the resilience of forest ecosystem services to changing disturbance regimes can be operationally quantified. The impacts of observed or simulated alterations on disturbance regime can be compared to HRV to determine whether they are likely to push the system outside its domain of operation, and are thus likely to exceed ecological resilience. Furthermore, recovery rates and successional trajectories under altered disturbance regimes can be evaluated to gain further insights into resilience, with high recovery rates along typical successional pathways being an indicator for strong attractors and high resilience. However, we also note that high rates of recovery of certain system properties (e.g. tree canopy closure) are not necessarily the best indicator of resilience for all ecosystem functions and services (Swanson *et al.* 2011; Beudert *et al.* 2015). Notwithstanding the fact that meaningful indicators might vary across systems and spatial scales, these general concepts of assessing and quantifying resilience to changing disturbance regimes can be applied in the context of a wide range of ecosystems and services.

However, resilience is a dynamic property, and climate change might not only change the disturbance regime (forcing the system towards the edges or even beyond its basin of attraction) but also impact the range of variability and recovery rates of an ecosystem (Fig. 2). Although the concept of the HRV was initially conceived as a stationary or quasi-equilibrium concept, we thus also need to explicitly consider the future range of variation (Duncan, McComb & Johnson 2010) resulting from the combined effects of global change to describe future system resilience. Although climate change is likely to increase pressure on ecosystem services, its effects on ecological resilience can be both positive (e.g. when increased productivity in high elevation areas leads to faster recovery of C stocks after disturbance) and negative (e.g. where systems become increasingly water-limited, leading to shifts in species composition or ecosystem function).

Furthermore, societies are also changing, and with them both the demand for ecosystem services and the ability to adapt to changes in their provisioning are changing over time. In order to assess future resilience of ecosystem services, also the future social range of variability (Duncan, McComb & Johnson 2010) and corresponding changes in social preferences and acceptance of ecosystem states need to be considered (Fig. 2).

Fostering resilience to changing disturbance regimes

PRINCIPLES

To foster resilience we suggest the following management principles:

Manage dynamically and experimentally—This is accomplished through commitment to adaptive management over several decades, including feedbacks from monitoring (Dale *et al.* 2001). Such adaptive feedbacks are particularly important considering the above-described dynamic nature of disturbance regimes *and* resilience properties (Fig. 2). They also enable management to adjust to shifting societal values and accommodate the changing needs for ecosystem services.

Manage for process—Management should focus on maintaining or enhancing ecological processes and functional characteristics, rather than specific structures and species compositions. Changes in disturbance regimes will likely alter forest structure and composition, but the processes relevant in the context of locally important ecosystem services (e.g. productivity in the context of C storage, water filtering and retention in the context of freshwater provisioning) might persist despite these changes (e.g. Beudert *et al.* 2015). Also, a focus on maintaining ecosystem functioning and processes could help ecosystem managers to accommodate changes in societal preferences.

Consider trade-offs and conflicts—Integrate ecological and socioeconomic sensitivities into management planning to provide a realistic context for considering different options for ecosystem services provisioning. Changing disturbance regimes affect ecosystem properties and processes at multiple levels, which is why assessing resilience needs to consider multiple indicators from the ecological and social spheres. Likewise, trade-offs and conflicting signals are possible and need to be addressed in management [e.g. increasing disturbance decreases C storage but increases albedo and thus has simultaneous positive and negative effects on the climate regulation function of forests (Thom & Seidl 2015)].

Prioritize—Resource managers have many choices but minimal financial and human resources, so prioritizing areas that are crucial for ecosystem services provisioning and will be most affected by changing disturbance regimes is critical. Likewise, identifying and prioritizing treatments that are likely to work in a range of possible futures will help address uncertainty (Millar, Stephenson & Stephens 2007).

Manage for realistic outcomes—Projects that are currently highly optimized for a specific (and usually narrow) set of ecosystem services may have a higher failure rate in a changing environment. In the face of altered disturbance regimes, it will become increasingly important to assess the viability of management goals and desired outcomes (Hobbs *et al.* 2006). Novel ecosystems hold the potential for new ecosystem services in the future, while some ecosystem services might be reduced through exceeded resilience and regime shifts (Reyer *et al.* 2015).

Treat disturbance as a management opportunity—Disturbance can cause profound changes in ecosystems, but also provides opportunities to apply adaptation strategies (Millar, Stephenson & Stephens 2007; Peterson, Halofsky & Johnson 2011). Plans, management projects and experiments should be designed and approved prior to large disturbances, in order not to default to simplified treatments post-disturbance. Furthermore, the complexity created by disturbances should be incorporated into the post-disturbance landscape and disturbance legacies maintained where possible, because they benefit biological diversity (Swanson *et al.* 2011) and foster recovery and system memory in the context of a multi-scale panarchy (Allen *et al.* 2014; Seidl, Rammer & Spies 2014).

PATHWAYS

These principles apply widely across the range of issues encountered in management planning under changing climate and disturbance regimes; specific pathways towards resilience in management, however, depend on local social and ecological contexts. Possible pathways towards resilience include:

Increasing structural diversity—This option focuses on increasing variety in structures at different scales (from within-stand heterogeneity to diversity in structures across large landscapes), avoiding ‘one size fits all’ management prescriptions that curtail heterogeneity (Millar, Stephenson & Stephens 2007). This includes applying forest thinning to increase variability in stand structure, as well as using a variety of harvest patterns, from single tree selection to patch cutting (Puettmann, Coates & Messier 2009; Nagel, Svoboda & Kobal 2014). Allowing fires to burn unsuppressed may in some cases emulate landscape patterns that are more congruent with their domain of natural variation (Hessburg & Agee 2003; Stephens *et al.* 2013), and thus help to put them in their historic basin of attraction (Fig. 1). However, trade-offs need to be considered between using disturbances to increase long-term resilience and potential short-term negative effects on selected ecosystem services (Seidl 2014).

Increasing species diversity—Resource managers can ‘hedge their bets’ by diversifying the phenotypic and genotypic template on which climate and disturbance interact. Species diversity increases the response diversity to changing environmental conditions (Mori, Furukawa & Sasaki 2013), and buffers the effects of larger and more frequent disturbances on ecosystem functioning (Silva Pedro, Rammer & Seidl 2015), supporting ecosystem services provisioning under changing disturbance regimes.

Increasing the spatial scope of management—Increasing the size of management units to thousands or tens of thousands of hectares across biogeographic entities such as watersheds will decrease ‘administrative fragmentation’ over space and time, and improve the likelihood of accomplishing objectives also under increasing disturbances (Smith & Lenhart 1996). For example, large strategically located blocks of forest land subjected to fuel treatments will reduce fire spread more effectively than smaller, randomly located units, helping to create fire-resilient landscapes. Where such a large spatial scope of management is not possible due to a small-scaled, heterogeneous ownership structure, coordination across ownerships and collectivization of risk (e.g. through insurance) should be considered to hedge against the risk of a complete loss of ecosystem services for individual landowners. Cross-border initiatives can help to increase the leverage of ecosystem management in the face of increasingly large-scale disturbance events (Heurich *et al.* 2010).

Matching infrastructure to expected future conditions—Forest management infrastructure, such as roads and drainages, need to accommodate future disturbance-related changes, for example in hydrology (Spittlehouse & Stewart 2003). It might also be beneficial to reconsider the design and density of road networks to make them more effective in responding to disturbances while reducing their impact on ecosystems. Furthermore, infrastructure such as wet storage facilities can help to buffer ecosystem services provisioning from negative effects such as the devaluation of salvaged timber from fungal infection and the need to sell timber in an oversaturated market (Gardiner *et al.* 2010).

Collaborating and educating—Working with a diversity of landowners, agencies and stakeholders will help define desired and/or socially accepted ecosystem conditions and build support for management aiming to increase the resilience of services to changing disturbance regimes. Furthermore, education on global change in general and the impact of changing disturbance regimes in particular should emphasize the role, potential and limitations of active management in adaptation. These activities can aid social adaptive capacity (Elbakidze *et al.* 2010) and the development of means to buffer decreasing ecosystem services provisioning after a disturbance in local communities (e.g. through redundancy). They can further empower individuals to take action, such as clearing brush around homes to reduce fire hazard.

While not in the focus of this contribution, another important response of management to changing disturbance regimes is to increase resistance and reduce undesirable disturbance risks and impacts (Millar, Stephenson & Stephens 2007; DeRose & Long 2014). Measures include increasing tree vigour and stability through thinning (Spittlehouse & Stewart 2003), selecting species and genotypes that are better adapted to the anticipated future conditions (Millar, Stephenson & Stephens 2007) and reducing rotation age to reduce risks. Such measures aiming to reduce risk are complementary to those focusing on resilience, although trade-offs can complicate a joint implementation. Under high uncertainty, resilience is a more robust strategy than anticipating and mitigating (poorly understood and unpredictable) risks (Seidl 2014).

Conclusions and Outlook

Towards the implementation of ‘resilience thinking’ in disturbance management, we identify three challenges that should be addressed in future work:

A better quantitative understanding of resilience to changing disturbance regimes

We propose measurable, well-defined indicators to describe resilience to changing disturbance regimes, such as range of variation (describing the basin of attraction, cf. ecological resilience) and recovery rate (as an indicator of engineering resilience). Because many systems lack the information required to quantify these properties, future research should focus on an operational quantification of resilience as a prerequisite for implementation in management. In the context of ecosystem services, better integration of social and ecological dimensions of resilience is needed, that is addressing forests as coupled human and natural systems (Spies *et al.* 2014).

Testing and implementing measures to sustain ecosystem services in the face of changing disturbance regimes

Based on experiences and suggestions in the literature, we compiled principles and pathways towards fostering resilience in ecosystem management. Good examples are needed for implementing these ideas and integrating them into forestry practice. Scientists in cooperation with managers and stakeholders need to scrutinize the specific efficacy of individual management measures and evaluate trade-offs between their effects on multiple ecosystem services. Only if the benefits of resilience-focused management in addressing changing disturbance regimes are clearly identified and communicated with managers and stakeholders will a wide implementation of such measures be successful. Because temporal and spatial scales of relevance in the context of resilience often exceed those of management, a stronger consideration of model-based projections will be needed in the future (Seidl *et al.* 2013).

A broad exploration of novel futures

Both disturbance agents and ecosystem services might vary in the future, that is the answers to the questions ‘resilience of what, to what’ are subject to change. Examples include the possibility of invasive non-native species acting as novel disturbance agents, as well as a rapid change in societal needs. Because the time horizons of forest management decisions are decades to centuries, it is advisable to actively explore scenarios of novel ecosystems and novel societies, and accommodate uncertainties and surprises more centrally into management planning.

Acknowledgements

R. Seidl acknowledges support from the Austrian Science Fund (P25503-B16) as well as from a Marie Curie Career Integration Grant of the European Community (PCIG12-GA-2012 334104). This paper is the result of a session held at the XXIV IUFRO World Congress in Salt Lake City, UT, USA, on 9 October 2014. We thank M.-J. Schelhaas and two anonymous reviewers for helpful comments on earlier versions of the manuscript.

References

Aldersley A, Murray SJ, Cornell SE. Global and regional analysis of climate and human drivers of wildfire. Science of the Total Environment. 2011; 409:3472–3481. [PubMed: 21689843]

Allen CR, Angeler DG, Garmestani AS, Gunderson LH, Holling CS. Panarchy: theory and application. Ecosystems. 2014; 17:578–589.

Bentz BJ, Régnière J, Fettig CJ, Hansen EM, Hayes JL, Hicke JA, Kelsey RG, Negrón JF, Seybold SJ. Climate change and bark beetles of the western United States and Canada: direct and indirect effects. BioScience. 2010; 60:602–613.

Beudert B, Bässler C, Thorn S, Noss R, Schröder B, Dieffenbach-Fries H, Foullois N, Müller J. Bark beetles increase biodiversity while maintaining drinking water quality. Conservation Letters. 2015; doi: 10.1111/conl.12153

Biggs R, Schlüter M, Biggs D, Bohensky EL, BurnSilver S, Cundill G, et al. Toward principles for enhancing the resilience of ecosystem services. Annual Review of Environment and Resources. 2012; 37:421–448.

Brand FS, Jax K. Focusing the meaning(s) of resilience: resilience as a descriptive concept and a boundary object. Ecology and Society. 2007; 12:23.

Burrows MT, Schoeman DS, Buckley LB, Moore P, Poloczanska ES, Brander KM, et al. The pace of shifting climate in marine and terrestrial ecosystems. Science. 2011; 334:652–655. [PubMed: 22053045]

Carpenter SR, Turner MG. Hares and tortoises: interactions of fast and slow variablesin ecosystems. Ecosystems. 2001; 3:495–497.

Carpenter S, Walker B, Anderies JM, Abel N. From metaphor to measurement: resilience of what to what? Ecosystems. 2001; 4:765–781.

Carpenter SR, Mooney HA, Agard J, Capistrano D, Defries RS, Díaz S, et al. Science for managing ecosystem services: beyond the Millennium Ecosystem Assessment. Proceedings of the National Academy of Sciences of the United States of America. 2009; 106:1305–1312. [PubMed: 19179280]

Creeden EP, Hicke JA, Buotte PC. Climate, weather, and recent mountain pine beetle outbreaks in the western United States. Forest Ecology and Management. 2014; 312:239–251.

Dale VH, Joyce LA, Mcnulty S, Neilson RP, Ayres MP, Flannigan MD, et al. Climate change and forest disturbances. BioScience. 2001; 51:723–734.

DeRose RJ, Long JN. Resistance and resilience: a conceptual framework for silviculture. Forest Science. 2014; 60:1–8.

Duncan SL, McComb BC, Johnson KN. Integrating ecological and social ranges of variability in conservation of biodiversity: past, present, and future. Ecology and Society. 2010; 15:1–10. art.5.

Elbakidze M, Angelstam PK, Sandstrom C, Axelsson R. Multi-stakeholder collaboration in Russian and Swedish model forest initiatives: adaptive governance toward sustainable forest management? Ecology and Society. 2010; 15:13.

Embrey S, Remais JV, Hess J. Climate change and ecosystem disruption: the health impacts of the North American rocky mountain pine beetle infestation. American Journal of Public Health. 2012; 102:818–827. [PubMed: 22420788]

Flannigan M, Cantin AS, de Groot WJ, Wotton M, Newbery A, Gowman LM. Global wildland fire season severity in the 21st century. Forest Ecology and Management. 2013; 294:54–61.

Gardiner, B.; Blennow, K.; Carnus, J.; Fleischer, P.; Ingemarson, F.; Landmann, G., et al. Destructive Storms in European Forests: Past and Forthcoming Impacts. EFIATLANTIC, European Forest Institute; Cestas, France: 2010.

Gutschick VP, BassiriRad H. Extreme events as shaping physiology, ecology, and evolution of plants: toward a unified definition and evaluation of their consequences. New Phytologist. 2003; 160:21–42.

Hamrick J. Response of forest trees to global environmental changes. Forest Ecology and Management. 2004; 197:323–335.

Hessburg PF, Agee JK. An environmental narrative of Inland Northwest United States forests, 1800–2000. Forest Ecology and Management. 2003; 178:23–59.

Heurich, M.; Beudert, B.; Rall, H.; Krenová, Z. National parks as model regions for interdisciplinary long-term ecological research: the Bavarian Forest and Šumavá National Parks underway to transboundary ecosystem research. In: Müller, F.; Baessler, C.; Schubert, H.; Klotz, S., editors. Long-term Ecological Research. Between Theory and Application. Springer; Dordrecht: 2010. p. 327-344.

Hicke JA, Jenkins JC. Mapping lodgepole pine stand structure susceptibility to mountain pine beetle attack across the western United States. Forest Ecology and Management. 2008; 255:1536–1547.

Hobbs RJ, Arico S, Aronson J, Baron JS, Bridgewater P, Cramer VA, et al. Novel ecosystems: theoretical and management aspects of the new ecological world order. Global Ecology and Biogeography. 2006; 15:1–7.

Holling, CS.; Gunderson, LH. Resilience and adaptive cycles. Panarchy. Understanding the Transformations in Human and Natural Systems. Gunderson, LH.; Holling, CS., editors. Island Press; Washington, DC, USA: 2002. p. 25-62.

Holling CS, Meffe GK. Command and control and the pathology of natural resource management. Conservation Biology. 1996; 10:328–337.

IPCC. Managing the Risks of Extreme Events and Disasters to Advance Climate Change Adaptation. Field, CB.; Barros, V.; Stocker, TF.; Qin, D.; Dokken, DJ.; Ebi, KL.; Mastrandrea, MD.; Mach, KJ.; Plattner, GK.; Allen, SK.; Tignor, M.; Midgley, PM., editors. Cambridge University Press; Cambridge: 2012. p. 582

Keane RE, Hessburg PF, Landres PB, Swanson FJ. The use of historical range and variability (HRV) in landscape management. Forest Ecology and Management. 2009; 258:1025–1037.

Knutson TR, McBride JL, Chan J, Emanuel K, Holland G, Landsea C, et al. Tropical cyclones and climate change. Nature Geoscience. 2010; 3:157–163.

Kurz WA, Dymond CC, Stinson G, Rampley GJ, Neilson ET, Carroll AL, Ebata T, Safranyik L. Mountain pine beetle and forest carbon feedback to climate change. Nature. 2008; 452:987–990. [PubMed: 18432244]

Littell JS, McKenzie D, Peterson DL, Westerling AL. Climate and wildfire area burned in western U.S. ecoprovinces, 1916–2003. Ecological Applications. 2009; 19:1003–1021. [PubMed: 19544740]

MA. Ecosystems and Human Well-Being: Synthesis. Millenium Ecosystem Assessment. Island Press; Washington, DC: 2005.

Merschel AG, Spies TA, Heyerdahl EK. Mixed-conifer forests of central Oregon: effects of logging and fire exclusion vary with environment. Ecological Applications. 2014; 24:1670–1688.

Mikkelson KM, Dickenson ERV, Maxwell RM, McCray JE, Sharp JO. Water-quality impacts from climate-induced forest die-off. Nature Climate Change. 2013; 3:218–222.

Millar CI, Stephenson NL, Stephens SL. Climate change and forests of the future: managing in the face of uncertainty. Ecological Applications. 2007; 17:2145–2151. [PubMed: 18213958]

Mori AS, Furukawa T, Sasaki T. Response diversity determines the resilience of ecosystems to environmental change. Biological Reviews. 2013; 88:349–364. [PubMed: 23217173]

Nagel TA, Svoboda M, Kobal M. Disturbance, life history traits, and dynamics in an old-growth forest landscape of southeastern Europe. Ecological Applications. 2014; 24:663–679. [PubMed: 24988767]

Nash KL, Allen CR, Angeler DG, Barichievy C, Eason T, Garmestani AS, et al. Discontinuities, cross-scale patterns, and the organization of ecosystems. Ecology. 2014; 95:654–667. [PubMed: 24804450]

Pausas JG, Fernández-Muñoz S. Fire regime changes in the Western Mediterranean Basin: from fuel-limited to drought-driven fire regime. Climatic Change. 2012; 110:215–226.

Peters EB, Wythers KR, Bradford JB, Reich PB. Influence of disturbance on temperate forest productivity. Ecosystems. 2013; 16:95–110.

Peterson, DL.; Halofsky, J.; Johnson, MC. Managing and adapting to changing fire regimes in a warmer climate. In: McKenzie, D.; Miller, C.; Falk, D., editors. The Landscape Ecology of Fire. Springer; New York: 2011. p. 249-267.

Prestemon JP, Holmes TP. Market dynamics and optimal timber salvage after a natural catastrophe. Forest Science. 2004; 50:495–511.

Puettmann, KJ.; Coates, KD.; Messier, C. A Critique of Silviculture: Managing for Complexity. Island Press; Washington, DC, USA: 2009.

Reyer CPO, Brouwers N, Rammig A, Brook BW, Epila J, Grant RF, et al. Forest resilience and tipping points at different spatio-temporal scales: approaches and challenges. Journal of Ecology. 2015; 103:5–15.

Seidl R. The shape of ecosystem management to come: anticipating risks and fostering resilience. BioScience. 2014; 64:1159–1169. [PubMed: 25729079]

Seidl R, Rammer W, Spies TA. Disturbance legacies increase the resilience of forest ecosystem structure, composition, and functioning. Ecological Applications. 2014; 24:2063–2077. [PubMed: 27053913]

Seidl R, Schelhaas M-J, Lexer MJ. Unraveling the drivers of intensifying forest disturbance regimes in Europe. Global Change Biology. 2011; 17:2842–2852.

Seidl R, Eastaugh CS, Kramer K, Maroschek M, Reyer C, Socha J, Vacchiano G, Zlatanov T, Hasenauer H. Scaling issues in forest ecosystem management and how to address them with models. European Journal of Forest Research. 2013; 132:653–666.

Seidl R, Schelhaas M-J, Rammer W, Verkerk PJ. Increasing forest disturbances in Europe and their impact on carbon storage. Nature Climate Change. 2014; 4:806–810.

Sheppard S, Picard P. Visual-quality impacts of forest pest activity at the landscape level: a synthesis of published knowledge and research needs. Landscape and Urban Planning. 2006; 77:321–342.

Silva Pedro M, Rammer W, Seidl R. Tree species diversity mitigates disturbance impacts on the forest carbon cycle. Oecologia. 2015; 177:619–630. [PubMed: 25526843]

Smith JB, Lenhart SS. Climate change adaptation policy options. Climate Research. 1996; 6:193–201.

Soja AJ, Tchebakova NM, French NHF, Flannigan MD, Shugart HH, Stocks BJ, et al. Climate-induced boreal forest change: predictions versus current observations. Global and Planetary Change. 2007; 56:274–296.

Spies TA, White EM, Kline JD, Fischer AP, Ager A, Bailey J, Bolte J, Koch J. Examining fire-prone forest landscapes as coupled human and natural systems. Ecology and Society. 2014; 19:1–14. art9.

Spittlehouse DL, Stewart RB. Adaptation to climate change in forest management. BC Journal of Ecosystems and Management. 2003; 4:1–11.

Stephens SL, Agee JK, Fulé PZ, North MP, Romme WH, Swetnam TW, Turner MG. Managing forests and fire in changing climates. Science. 2013; 342:41–42. [PubMed: 24092714]

Stephens SL, Burrows N, Buyantuyev A, Gray RW, Keane RE, Kubian R, et al. Temperate and boreal forest mega-fires: characteristics and challenges. Frontiers in Ecology and the Environment. 2014; 12:115–122.

Swanson ME, Franklin JF, Beschta RL, Crisafulli CM, DellaSala DA, Hutto RL, Lindenmayer DB, Swanson FJ. The forgotten stage of forest succession: early-successional ecosystems on forest sites. Frontiers in Ecology and the Environment. 2011; 9:117–125.

Temperli C, Bugmann H, Elkin C. Cross-scale interactions among bark beetles, climate change, and wind disturbances: a landscape modeling approach. Ecological Monographs. 2013; 83:383–402.

Tepley AJ, Swanson FJ, Spies TA. Fire-mediated pathways of stand development in Douglas-fir/western hemlock forests of the Pacific Northwest, USA. Ecology. 2013; 94:1729–1743. [PubMed: 24015517]

Thom D, Seidl R. Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. Biological Reviews. 2015; doi: 10.1111/brv.12193

Turner MG. Disturbance and landscape dynamics in a changing world. Ecology. 2010; 91:2833–2849. [PubMed: 21058545]

Usbeck T, Wohlgemuth T, Dobbertin M, Pfister C, Bürgi A, Rebetez M. Increasing storm damage to forests in Switzerland from 1858 to 2007. Agricultural and Forest Meteorology. 2010; 150:47–55.

Weed AS, Ayres MP, Hicke JA. Consequences of climate change for biotic disturbances in North American forests. Ecological Monographs. 2013; 83:441–470.

Westerling AL, Hidalgo HG, Cayan DR, Swetnam TW. Warming and earlier spring increase western U.S. forest wildfire activity. Science. 2006; 313:940–943. [PubMed: 16825536]

Westerling AL, Turner MG, Smithwick EAH, Romme WH, Ryan MG. Continued warming could transform Greater Yellowstone fire regimes by mid-21st century. Proceedings of the National Academy of Sciences of the United States of America. 2011; 108:13165–13170. [PubMed: 21788495]

Zurbriggen N, Nabel JEMS, Teich M, Bebi P, Lischke H. Explicit avalanche-forest feedback simulations improve the performance of a coupled avalanche-forest model. Ecological Complexity. 2014; 17:56–66.

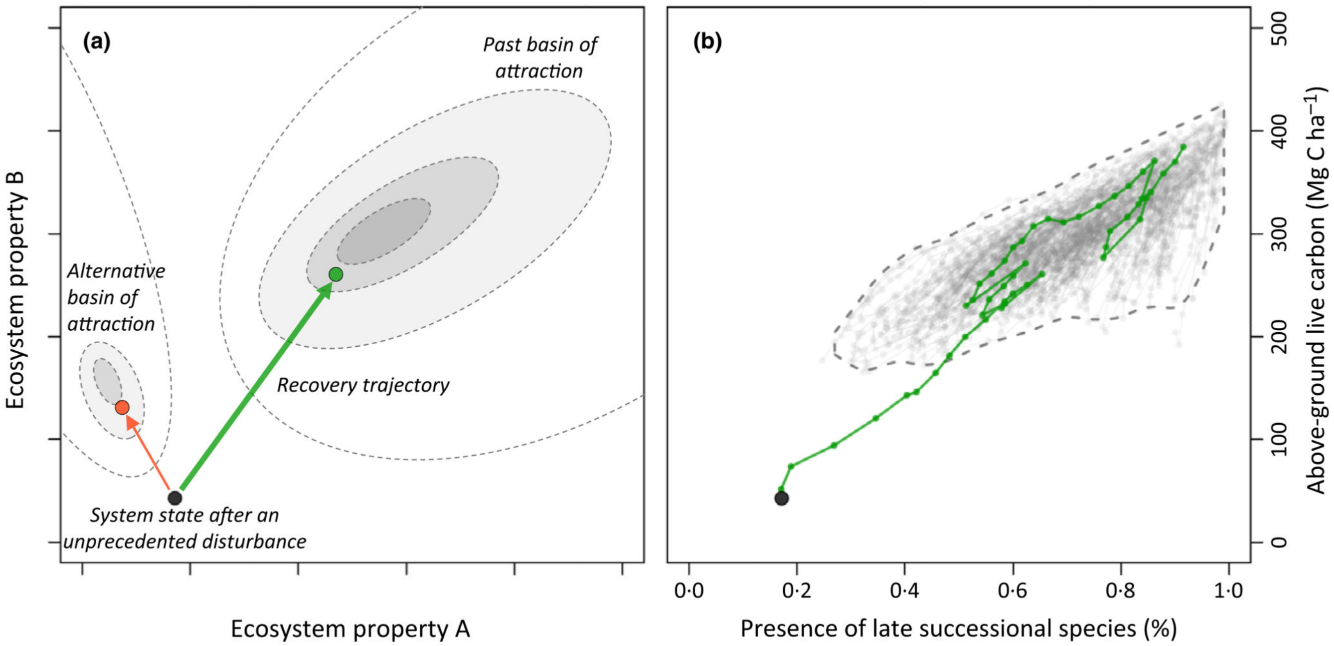

Fig. 1.

(a) Schematic visualization of the constituents characterizing an ecosystem's resilience to novel disturbance regimes. Changes in the disturbance regime can push the forest system (dot) outside of its past basin of attraction (defined as grey ovals). The resilience to such a change describes if (ecological resilience) and how fast (engineering resilience) the system returns to the past basin of attraction (e.g. a closed forest; green trajectory), or if instead the system shifts to a state within an alternative basin of attraction, such as a shrubland (red trajectory). (b) Application of this concept for a forest landscape in western Oregon, USA. The location and size of the past attractor is described by the historical range of variability (HRV), here illustrated for two crucial properties in the context of ecosystem services, the presence of late-seral species and above-ground live carbon storage. Values are derived by means of simulations with a forest landscape model (representing a total of 30 000 simulation years). The system state in 10-year time-steps is illustrated by circles (semi-transparent to display local point density), and the HRV is approximated as a convex hull around these states (dashed line). After an unprecedented disturbance (here a mega-fire affecting nearly the entire landscape with high severity), the system is temporarily pushed outside of its past basin of attraction (black circle). Yet, this disturbance does not exceed a tipping point towards an alternative state here: the simulated 500-year recovery trajectory (green) shows that after a brief reorganization phase, the system re-converges with its past HRV (and thus is ecologically resilient). It, however, takes more than eight decades for the two ecosystem properties to recover to historic values, which is an indication of only moderate engineering resilience (source: Seidl, Rammer & Spies 2014).

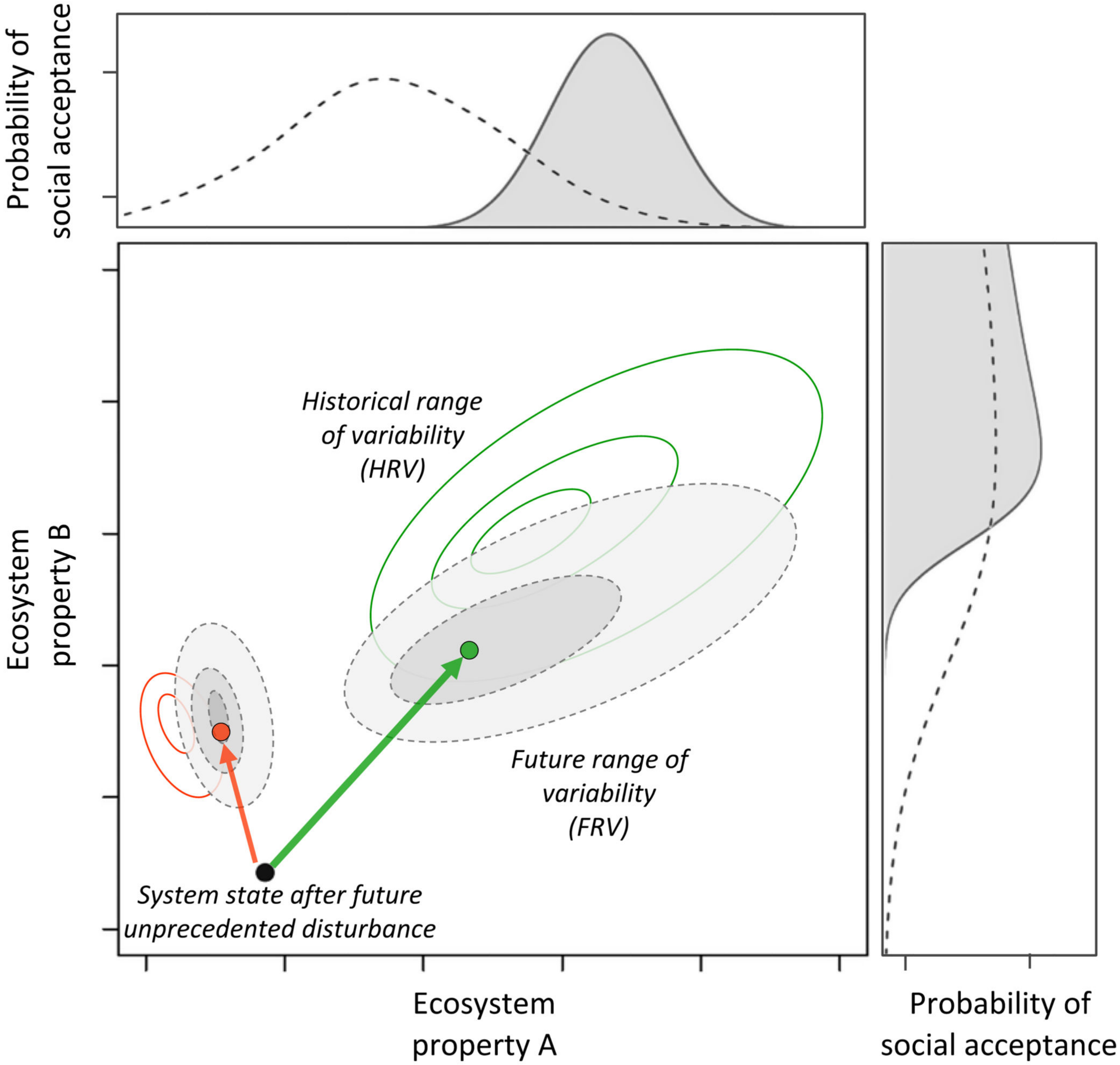

Fig. 2.

Climate change is likely to change the system's attractor landscape. The speed of recovery (arrow) as well as the location, size and depth of the past basins of attraction (red and green ovals) could be modified by climate change (grey ovals). To assess the effect of these changes on ecosystem service provision, they need to be evaluated in the context of the social acceptance of the changed ecosystem properties. Here, a recovery towards a future modified basin of attraction (green dot) would retain the system within the social range of variability (Duncan, McComb & Johnson 2010), although the probabilities of social acceptance of the new state are considerably decreased compared to the historical range of variability (cf. the grey marginal probabilities). A regime shift following an unprecedented disturbance (red dot) would result in a loss of ecosystem services and push the system outside of the range of socially accepted system states. In response, societies can either try to compensate this loss (e.g. through technology), adapt their preferences (indicated here by a second set of dashed marginal probabilities) or engage in restoration efforts aiming to reverse the ecological regime shift brought about by the unprecedented disturbance.