

Available online at www.sciencedirect.com



Forest Ecology and Management

Forest Ecology and Management 242 (2007) 541-552

www.elsevier.com/locate/foreco

The usefulness of stability concepts in forest management when coping with increasing climate uncertainties

Per Bodin*, Bo L.B. Wiman

Environmental Science Section, Department of Biology and Environmental Science, Kalmar University, SE-39182 Kalmar, Sweden Received 14 February 2006; received in revised form 7 November 2006; accepted 21 January 2007

Abstract

Forest management is challenged by increasing needs to adapt practices to future climate change likely to be characterised by a changing frequency of extreme weather events, in turn in uncertain ways resulting in more pronounced disturbances on forests. In this paper, we explore the extent to which insights acquired by ecological theory, in particular with respect to stabilising properties, have been of use to forest management theory and practice, and whether these insights can be applied in a valuable way to forest managers in view of increasingly uncertain disturbance regimes. We find it highly unlikely that there exists one strategy option that can optimise for all types of disturbances and that can also maximise for all other demands placed on forest management. Therefore, management needs to be related to the most relevant disturbances; or, alternatively, a multitude of management options may be combined as an insurance strategy. Possibly, heterogeneous/mixed forest communities could insure against climate-change related pressures. We also note the importance of spatio-temporal scales when relating disturbance to stability, and thus the needs for advancing modelling in that field to assist in developing management strategies for the future.

Keywords: Forests; Stabilising properties; Adaptive management; Climate change; Forest fires; Wind-fellings; Parasite attacks

1. Introduction

A prevailing view underpinning forest management has been that forests, and other ecological systems, possess an innate tendency to return to equilibrium irrespective of the type of disturbance and an ensuing perception of forests as capable of providing stable productivity over time (Farrell et al., 2000). Lately there has been a paradigmatic shift in ecological theory towards perceptions invoking more clearly the dynamic properties of ecological systems (e.g., Wiman, 1991), including forests, conducive to more comprehensive forest system management instead of optimising solely for timber production (Niemelä, 1999; Bengtsson et al., 2000; Führer, 2000). This conceptual change can be linked to an increased ecological interest in ecosystem services (and not only ecological goods, such as fibres) and the connection between different services and biodiversity (Loreau, 2000; Loreau et al., 2001). Here, it merits mention that the concept of ecological services is far from new; it was formulated and advocated already in the 1970s (Vlijm and Likens, 1975) and, in Sweden, was communicated to the Parliamentary Committee on Environment and Natural Resources Management in the 1980s (Wiman and Holst, 1982). One such ecosystem service that is being debated is ecosystem stability. However, it might not be simple, or in some cases even valid, to see stability as a *reliable* ecosystem service. Nevertheless, this increased interest in biodiversity and ecosystem services has led to an actualisation of the longstanding stability/diversity debate, and although still controversial among ecologists, different concepts of stability and diversity are being used in forestry and ecosystem management.

The changing view of forests and forestry places additional and multiple-use demands on forest management, thus making it important not only to ensure forest productivity but also other services contained by, and provided by, the entire forest system, such as decomposition; nutrient cycling; water regulation; recreational, conservational, and aesthetic functions; and – as an emerging and quite complex additional societal function – carbon sequestration under the Kyoto Protocol. This will probably lead to needs for accepting trade-offs when choosing management strategies, since no management option is likely to maximise all forest ecosystem functions. For example, strategies for managing a forest community in order to maximise its

^{*} Corresponding author. Tel.: +46 480 44 62 52; fax: +46 480 44 73 05. *E-mail address:* per.bodin@hik.se (P. Bodin).

^{0378-1127/\$ –} see front matter \odot 2007 Elsevier B.V. All rights reserved. doi:10.1016/j.foreco.2007.01.066

atmospheric-carbon sink strength might not easily, if at all, be reconciled with strategies aimed at maximising biodiversity (Bäckstrand and Lövbrand, 2006).

Uncertainties of many types, connected to future climate, further compound the management challenge. Most of the climate science community agree that even with drastic mitigation measures taken, the global mean tropospheric temperature is rising and will continue to do so. However, uncertainties regarding how climate will shift on a regional-tolocal scale remain large (Houghton et al., 2001; Rummukainen et al., 2004) and an increase in extreme events throughout Europe seems likely (Hulme and Carter, 2000). For example, long warm summers could lead to the parasite Ips typographus having two generations during one summer meaning an increased probability of an outbreak (Harding and Ravn, 1985; Jönsson, 2004). The recent occurrence of some extreme weather events in Europe has brought issues of adaptation of forestry to future climate change on the agenda. Examples of such events are the 2005 storm "Gudrun" that caused largescale direct damages to Swedish forests where about 75 million m³ of forest were wind-felled (Niklasson and Nilsson, 2005, p. 102) and the 2003 summer heat and drought that caused productivity reduction, and a function-shift from carbon sink to carbon source, over much of Europe (Ciais et al., 2005).

Another important disturbance – also potentially strongly geared to meteorological change – is forest fire, thus posing additional risk-management problems to forestry. Taking Sweden as an exemplifying case, most of the terrain is covered by flammable coniferous trees, ericaceous dwarf-shrubs and mosses (Granström, 1998). During the mid-1970s fire was not considered a serious problem, and the collection of fire statistical data was temporarily abandoned in 1975, but resumed in 1992 (Granström, 1998). Between 1992 and 1996 the average area burned was 2500 ha year⁻¹ (FAO, 2005). In 1992 and 1994, the number of fires, and the areas burned, were exceptionally high.

A change in forest management from optimising for sustainable yield of a well-defined good (such as fibre; wood fuel) towards optimising for a broad range also of forest services, in combination with measures to insure against meteorological manifestations of a changing climate, undoubtedly presents fundamentally new challenges. It warrants special emphasis (e.g., Parry, 1986; Ciais et al., 2005) that these manifestations might involve not only shifts in the long-term averages of meteorological parameters but also changes to the frequency distribution curves. These might broaden, in other cases might narrow, and in still other cases might become skewed, so that the frequency of anomalous weather events in some cases might decrease and in other cases might increase. In addition, the amplitude of parameter oscillations might change substantially. Increased demands for a more holistic and multiple-use management perspective, and increased uncertainties, thus make decision-making about management strategies more difficult.

There are therefore substantial needs for analyses of what ecological theory can contribute. In this paper, we investigate how different stability concepts have been, and could be, used in forest management in relation to this combination of expanding demands on forest services and climate-change related disturbances. We base our investigation on fundamental concepts involved (Section 2), critically explore their usability in forest ecosystem management (Section 3), and then address needs for enhancing stabilising properties of managed forests (Section 4).

2. The stability and diversity concepts

Inevitably, the management of ecological systems, not in the least forests, interacts with a broader scientific – and thus dynamic and often contentious - framework of ecological systems theory. In population ecology, biomathematical analyses of stability of theoretical populations subjected to inter- or intraspecific competition date back at least to Lotka (1924, 1956). A notion that "diversity begets stability" is of particular management interest, and was the prevailing view in community ecology from the 1950s (Elton, 1958; Odum, 1963, 1969; Leps et al., 2001; Leps, 2004; for review and analysis see Goodman, 1975; Wiman, 1991) until challenged by among others May (1973, p. 74). He showed that in mathematical representations (i.e., models) of multi-species communities the stabilising capability of the system decreased with increasing diversity (in this case in terms of number of interacting species). Among recent treatises on relationships between biodiversity and ecosystem functioning, including stability, are Walker (1992), Tilman (1999), Loreau (2000), Loreau et al. (2001), Hooper et al. (2005) and Srivastava and Vellend (2005).

Besides the still common idea that stability (in some, often not stringently clarified, sense) increases with increasing diversity there exist four general lines of thought: the driver/ passenger hypothesis; the rivets hypothesis; the idiosyncratic hypothesis; and the null hypothesis (no relationship). The driver/passenger (or redundancy) hypothesis (Walker, 1992; Lawton, 1994; Naeem, 1998) suggests that beyond a certain minimum number of species required for maintaining ecosystem function other species are redundant in their roles. In their "rivets hypothesis" Ehrlich and Ehrlich (1981) assume that all species make a contribution to ecosystem function similar to rivets on an airplane where, if rivets are lost, the plane might still function but will eventually crash; i.e., if species are lost, their function over at least a period of time may be compensated for by other species with similar functions. In the idiosyncratic hypothesis, diversity is believed to affect stability, but the effect and magnitude of a change in diversity are thought to be unpredictable (Lawton, 1994).

Several more specific hypotheses exist, for instance with respect to differing conceptualisations of "stability" such as variability (e.g., Tilman, 1999; McCann, 2000), which, however, does not necessarily relate to stringent mathematical terminology involving *stabilising capabilities*—which constitute the concept of interest to management and therefore warrants a brief analysis prior to exploring its applicability. For this contribution, it is beyond our scope to probe into

mathematical analyses and we confine ourselves to providing references wherein such analyses are available.

2.1. A brief overview of stability concepts

In ecology, stability concepts initially stemming from the physics and technology realms have been adopted by ecologists and the discussion about the usefulness of their application in this field will continue (Wiman, 1991). In the mathematics and technology domains – in contrast to ecology realms – the systems described are well defined and the meaning of different types of stability is clear. Therefore, their use in those domains becomes straightforward, but following transfers to ecological

Table 1

Stability-concept categories and their definitions after Orians (1975)^a

(A) Constancy: A lack of change in some system parameter.Implies nothing about causation.

- (B) Trajectory stability (resilience): The capacity of a system to move towards some final end point or zone despite differences in starting points.
 - Strong organism-induced modifications of the physical environment.
 - All factors increasing elasticity.
- $\left(C\right)$ Persistence: The survival time of a system or some component of it.
 - Environmental heterogeneity in space and time.
 - Large patch sizes.
 - Constant physical environment.
 - High resource utilisation thresholds of predators.
- (D) Inertia (resistance): The ability of a system to resist external perturbations.
 - Environmental heterogeneity in space and time.
 - Greater phenotypic diversity of prey.
 - Multiplicity of energy pathways.
 - Intraspecific variability of prey.
 - High mean longevity of individuals of component species.
- (E) Elasticity: The speed with which the system returns to its former state following a perturbation.
 - High density dependence in birth rates.
 - Short life cycle of component species.
 - Capacity for high dispersal.
 - Strong migratory tendencies.
 - Generalized foraging patterns.
- (E) Amplitude (domain of attraction): The area, i.e., domain—over which a system is stable.
 - · Weak density-dependence in birth rates.
 - Intraspecific variability of component species.
 - Capacity for long-distance dispersal.
 - Broad physical tolerance.
 - Generalized harvesting capabilities.
 - Defence against predators not dependent on a narrow range of hiding places.
- (F) Cyclic stability: The property of a system to cycle or oscillate around some central point or zone.
 - High resource-utilisation thresholds.
 - Long lag times in response of species to changes in resource availability.
 - Heterogeneity of environment in space and time.

Where the definitions of Grimm and Wissel (1997) differ from Orians (1975) the former are written within brackets.

^a His view of how factors such as resource harvesting, competition, and predator–prey interactions affect the differing types of stability are marked with
in the table. Note that Orians remarks, non-trivially, that "factors decreasing these stabilities are generally the inverse of those increasing them".

systems questions arise about analogies being mistaken for identity; or as Grimm and Wissel (1997) put it: "Stability concepts derived from mathematics and physics are only suited to characterising the dynamic behaviour of simple dynamic systems, but ecological systems are not simple dynamic systems".

Several decades ago, Orians (1975) saw the problem with the multitude of stability concepts that existed and found that these could be sorted into one of six basic conceptual categories: constancy, trajectory stability, persistence, inertia, elasticity, amplitude and cyclic stability. Out of these, he (correctly, as we see it) discarded "constancy" as in fact conveying nothing about a system's dynamic response to a disturbance. Essentially (see Table 1), Orians (1975) and Grimm and Wissel (1997) therefore go "back to basics" outlined already by Lotka (1924, 1956). Grimm and Wissel (1997) employ a partly upgraded terminology which we will use in the following; their *resilience* is essentially the same as trajectory stability; inertia was named resistance; and amplitude was named domain of attraction. We also note that some studies indicate that ecosystems could have multiple attractors so that a disturbance might push the system into a new stable steady state (Holling, 1986; Scheffer et al., 2001). Interestingly, Orians (1975) also suggests how factors such as resource harvesting, competition, and predator-prey interactions affect the differing types of stability.

In epitome, the categorisations provided above emphasise the fact that for the concept of stability to take on a useful meaning the basis must be one of a system's *stabilising* properties. The observation that a system is *in equilibrium* reveals nothing about its stability properties, except that the system possesses an equilibrium state. But unless that information is complemented by knowledge on whether the system, in relation to a perturbation, is fragile in this state (and in unstable equilibrium) or robust (and in stable equilibrium), nothing can be said about the stabilising capability.

2.2. A brief overview of diversity concepts

The stability/diversity debate is not only compounded by the stability terminology; the biodiversity concept is at least as debated. There is an ongoing discussion in the ecology and conservation-biology communities (e.g., Walker, 1992), and biodiversity is also (as is "resilience"; see Bodin and Wiman, 2004) a term that has been politicised, and thus still more troublesome.

Among measures of biodiversity that are of proposed relevance to nature-conservation policies are species numbers at different scales (Whittaker, 1977) and genetic, organismal or ecological diversity (Harper and Hawksworth, 1995). Approaches that more clearly address not only structure but also its relationship with ecosystem functioning are those that emphasize keystone species or the number of functional groups (Lawton, 1994; Perry, 1994, pp. 515–521; Bengtsson, 1998) or that apply weighted indices such as Simpson's and Shannon's diversity indices (e.g., Begon et al., 1986). Here, we observe that Shannon's index is imported from mathematical information theory (Shannon and Weaver, 1949), and based on the concept of information entropy, valid only for systems that meet stringent demands on mathematical–physical properties (e.g., Gallager, 1968).

A quite different – and, as we, the authors, perceive it, more stringent - approach to conceptualising diversity is to combine the number of components (such as species) of a system with the degree of connectance between them (such as with respect to energy transfers between species in a food web). Many theories about stability assume that the components in the system are fully connected. This might not be a realistic assumption and the effect on the stability of a system of using different levels of connectance has been investigated by Gardner and Ashby (1970), who found that there is a clear relationship between the number of components that are connected, the strength of these connections, and the probability for unstable behaviour of the system. In essence, their results are in support of May's (1972) findings in the early 1970s and also relate to applications of chaos theory in ecology (Schaffer and Kot, 1985).

Patchiness, or fragmentation, in a forest community is also a measure of spatial diversity (Kareiva, 1987). This is in line with the tendency now in ecological theory to move on to modelling that more efficiently addresses spatio-temporal system properties (Dieckmann et al., 2000).

2.3. Some implications

Several authors (Orians, 1975; Pimm, 1984; Grimm and Wissel, 1997) have noted the problems with the widespread use of a huge variety of stability concepts. A statement such as "diversity begets stability" is simply too general to have any meaning (Pimm, 1984; Grimm and Wissel, 1997; Bengtsson, 1998; Schläpfer and Schmid, 1999). In addition, an "unstable" population on a small scale may well show "stability" on a larger scale (e.g., DeAngelis and Waterhouse, 1987; Kareiva, 1987; Kareiva and Wennergren, 1995; Dieckmann et al., 2000). Some notions of stability stem from the field of community ecology whereas most theories and models emanate from population ecology. Communication between these two subdisciplines has been "difficult and sometimes non-existent" (Loreau, 2000).

Advancing emerging theories used in patch dynamics and spatio-temporal modelling would clearly promote forest management strategies for forests subject to shifts in climate, as would adopting the checklist suggested by Grimm and Wissel (1997) who take into account: (1) level of description; (2) variable of interest; (3) reference state; (4) type of disturbance; (5) spatial scale; and (6) temporal scale.

3. The use of stability concepts in forest ecosystem management

From a forest-management point of view it thus appears that perceiving stability as a general ecosystem function poses problems. After all, a primary economic incentive of forest management is, and will inevitably continue to be, to produce fibre in quantities and qualities suited to the intended use. Additional specifications become necessary for stability aspects to find their appropriate context: ecological systems– functions of relevance are those that protect against different disturbances of a broadening range of societally important forest characteristics, such as stand biomass, species composition, carbon-sink capacity. And, indeed, forests are subject to many different forms of disturbances, mostly due to fluctuations in the physico-chemical environment, but also emanating from biotic factors in the ambient milieu.

3.1. The importance of defining disturbances

The ecological role of disturbances remains a long-standing and important topic in ecological theory. For instance, early work by Horn (1974) suggests that disturbances, as long as they are not in some sense too strong, contribute to diversity, whereas a high disturbance frequency might be conducive to reduced diversity. This can be compared with May (1975): "The thing which destabilizes man's agricultural monocultures is not so much their simplicity *per se*, as their lack of an evolutionary pedigree". Thus, the stability problem becomes meaningful only when it is embedded in the framework of disturbance regimes: the real issue at hand is therefore not the complex of "stability/diversity", but the full context of "stability/diversity/disturbance".

It is common, in mathematics and technology as well as in ecology, to categorise disturbances into press or pulse disturbance (Bengtsson et al., 2003), where a pulse disturbance is discrete in time and the press disturbance is chronic. The largest pulse disturbance to a forest is the clear-cutting of wood that causes the entire living tree biomass to be removed (excluding root fractions, unless whole-tree harvesting is applied). Other possible pulse disturbances are forest fires, extreme winds (causing overturning or snapping of stems), snowfall (that can lead to breakage of stems due to over-loading of heavy snow), rockslides (in mountainous regions) and parasite attacks (in terms of parasite populations growing from endemic to epidemic levels). Press disturbances affect forests in more subtle ways, such as via acidification, increases in tropospheric ozone, changes in temperature and precipitation occurring as manifestations of changes - be they man-made or not - in local, regional, or global climate, often causing ecosystem degradation (e.g., Hüttl and Schneider, 1998). Several potentially malign feedbacks might exist, inasmuch gradual deterioration, in turn, can cause the trees to become less resistant also to pulse disturbance. In addition, feedbacks between for instance climate-change parameters (such as temperature and UV-radiation regimes) and tropospheric chemistry (such as that of ground-near ozone) might turn pressure-types of disturbance into pulse-types, because of nonlinear mechanisms (in for example atmospheric chemistry) (e.g., Wiman, 2002; Karnosky et al., 2003). Although, in the following, we mainly focus on more direct disturbances, the above-given examples of more subtle and indirect impacts should be borne in mind precisely because they might feed back, through systemic non-linearities, to increased as well as decreased forest vulnerability due to more direct and in forestry more commonly addressed pulse impacts.

When discussing the stability of an ecosystem vis-à-vis a specific disturbance it is, in forestry, usually a pulse disturbance that is referred to. White and Pickett (1985, p. 7) define disturbance as being "any relatively discrete event in time that disrupts ecosystem, community or population structure and changes resources, substrate availability, or the physical environment", therefore essentially excluding press disturbance from the definition. Doing so is probably the most meaningful when discussing stability of systems since it is difficult to separate the effects of different press disturbances and, as noted above, these could be viewed as factors that may decrease the stability to a specific (pulse) disturbance. In the following, we address pulse disturbances unless otherwise stated.

3.2. Stability concepts as potentially applicable onto forest management

Research about different forms of disturbances has been intensively conducted within forestry, but – similar to ecosystem-stability research – has been theoretical rather than experimental, and therefore with only limited applications in forest management (Larsen, 1995). Instead, the interest in stability has emanated from its potential use in protecting individual trees against disturbances such as forest fires and insect outbreaks, and in managing forest ecosystems in order to make them more resistant to external disturbances or more resilient/elastic following a clear-cutting.

The "panarchy" concept (Holling, 2001) and the concept of adaptive cycles (Holling, 1986, 2001) address the dynamics of ecosystems, and have gained credibility in the forest ecosystem community (Bengtsson et al., 2000; Dorren et al., 2004). The panarchy concept involves dynamics on different spatial as well as temporal scales, and thus exemplifies an approach to differentiating between properties that might stabilise (or destabilise) a system despite unstable (or stable) behaviour of its sub-systems. In an adaptive cycle, the ecosystem becomes more complex, less variable and less "resilient" (sensu Holling, 1986) as it matures, eventually leading to a release of stored capital caused by a perturbation such as generated by fire, storm or pests (Holling, 1986, 2001). In an intensively managed forest ecosystem the trees will have reached the same degree of maturity, and the stand thus would have a homogeneity rarely observed in unmanaged forests. Therefore - according to these hypotheses - such a forest, subjected to "forced succession", would be more susceptible to disturbances whereas a natural forest ecosystem is patchier and hosts trees, as well as other biotic components, of differing ages. Here, it merits mention that Harper (1977, p. 707) emphasises the role of age distribution within a community: "[the] distribution of ages within a population may be one of the elements of diversity that contributes to the stability of the community - at least in the sense that it permits or denies the chance of rapid recovery after a disaster".

Some researchers claim that human-caused disturbances (such as logging) might be conducted in a manner that would

mimic natural disturbances in order to generate more heterogeneous forest landscapes (Niemelä, 1999; Bengtsson et al., 2000). This will be discussed further below.

3.3. Stability concepts in relation to specific disturbance regimes, and some implications

Stability concepts can be incorporated into forest management in a general way, so as to promote new principles at large, or they can be applied in relation to a particular disturbance such as with respect to snow accretion (Kato and Nakatani, 2000), insect outbreaks (Perry, 1994), rock-fall (Dorren et al., 2004) or - more commonly studied - in relation to forest fire (Brown et al., 2004; Kazanis and Arianoutsou, 2004; Perry et al., 2004; Harper et al., 2005), wind-fellings (Gardiner and Ouine, 2000; Gardiner et al., 2000; Mitchell, 2000; Ulanova, 2000; Cameron, 2002; Mason, 2002: Blennow and Sallnäs, 2004: Achim et al., 2005: Olofsson and Blennow, 2005), and clear-cutting (Halpern, 1988, 1989; De Grandpré and Bergeron, 1997; Selmants and Knight, 2003). A few cases also exist wherein stability/instability vis-à-vis specific disturbances (such as parasite outbreaks and their connections with meteorological factors and available leaf-area, and forestry practices with applications of parasite-combating chemicals) have been studied, resulting in recommendations towards basically new overarching principles and strategies as well as more specified management procedures (Holling, 1978; Ludwig et al., 1978).

For management purposes such as conservation, the speciescomposition stability may be more relevant (Halpern, 1988) than the much more studied mortality of individual trees under various specified disturbance regimes. Hence, the relevance of the basic stability concepts (Table 1) for analysing managed forests and for policymaking in forestry is not necessarily the same as for studying un-managed forests and for policymaking in nature-conservation management. This is because managed forests are characterised by "forced succession" towards "economically profitable climax stages" that differ significantly from "natural succession" towards "ecological climax stages" implying metabolic equilibrium.

In this context it needs to be observed that during succession - be it forced by management or resulting from natural processes – forest systems, as other ecological systems, are in continuous dynamic change a priori. This situation, if considered in strict mathematical terms, poses particular challenges to stability analysis inasmuch stringent concepts of equilibrium essentially emanate from models built on systems of ordinary differential equations that do not take changes in the system's structure into account. Much research is needed in this realm so as to improve forest-management capabilities to link fairly short-term dynamics to long-term change, including abilities to account for the balance between stochastic and deterministic processes for self-organisation of the system (a problem area often named "synergetics", see Haken, 1978). For instance, May (1999) notes that ecosystems are in tension between evolutionary forces (that tend to add species to efficiently exploit or subdivide every available niche) and dynamic forces (where an increased species number leads to greater dynamic fragility). That is, the dynamic (and thus stabilising) properties of a model of an ecological system at a given point t_n in time reflects the system's configuration at precisely t_n , but at time $t_n + \Delta$ (Δ in principle infinitesimally small) the system's configuration may differ, and the model needed to account for those changes may yield quite different stability properties (cf., Wiman and Holst, 1982). However, assuming that the succession of the forest system under study can be seen as sufficiently slow, the process can be perceived as occurring in identifiable stages. Each of these stages can then be subjected to stability considerations. Since concepts such as constancy (or its opposite, variability) and persistence tend to lack any stringent meaning for time-scales involved in a succession stage (except a hypothesized ecological climax), the concepts of major interest will be (cf., Table 1) "stability domain" (or domain of attraction), resilience, elasticity, and resistance.

3.4. The use of domain of attraction, resilience, and elasticity concepts in forest management

Clearly, the domain of attraction of a forest (in a given succession stage) is of major relevance to forest management, but is normally notoriously difficult to define already for the case when realistic mathematical models of the system exist, and is also very difficult to test empirically (cf., May, 1975). However, there are examples of successful forest management models partly allowing for identification of the domain of attraction, or at least thresholds at which the system transits ("flips") to a different behaviour (see Ludwig et al., 1978), i.e., undergoes a re-configuration resulting in new stability characteristics. Further progress along these lines would be highly important (not only with respect to forest systems) and – although calling for large and advanced cross-disciplinary research programmes – might well be accomplishable.

Resilience and elasticity are mainly used for analysing largescale disturbances to entire stands. After a stand-replacing disturbance, questions about the ability to return, and the speed of return if it occurs, to a reference state of for example stand biomass are relevant. Resilience and elasticity of naturally regenerated ecosystems are thought to be dependent on factors such as the sprouting of existent individuals; and on growth from existing seedlings, seeds in the seed bank, and dispersed seeds from the surrounding areas (e.g., Bormann and Likens, 1979, p. 105); factors essentially in line with Orians's (1975) suggestions in Table 1. Resilience of a managed forest stand to a fire disturbance can be defined as the ability to recover in the first place, such as with respect to re-gaining a degree of "control" of the nutrient cycles (a resilience aspect) and the speed of return to a certain state (such as in terms of biomass) after the disturbance.

In this context, when recovery and return to the original state are assumed a priori (which, as is implicit in the stabilitydomain concept, can be invalid an assumption, since the perturbation might be conducive to a "flip") it is important to observe the fundamental policy implications of elasticity. We observe that already in the 1970s means were suggested – but so

far have been remarkably little explored - by which it is possible to introduce the judgment of the observer into stability analyses (Harte, 1979). This can be accomplished through invoking various mathematical procedures, which for simplicity can be named weighting. Such procedures can be used to let the observer (such as a policy-maker) decide on which type of system-behaviour, in terms of elasticity, should be judged as more important than another, and have the advantage of making transparent a value-laden assessment of a system behaviour. Combining technical detail and stringency, in approaching ecosystem vulnerability and stability, with policy-relevant interpretations and applications would at least place rigorous demands on clarity and precision in defining the chain of concepts - including not only diversity-stability-disturbance perceptions, but also for instance socio-economic valuing of the system – that underpin final decision-making. Note that he type of problem is analogous to revealing policy perceptions of how a fairly short-lived but strong (high global-warming potential, GWP) greenhouse gas (such as methane) should be compared with a less harmful (low GWP per unit mass) but much more long-lived greenhouse gas such as carbon dioxide, and what time horizons (discount rates) are judged policy-relevant (cf., e.g., Lashof and Ahuja, 1990). Fig. 1 provides an example.

Among examples of disturbances of particular interest here are clear-cutting and forest fires. The recovery (re-initialisation of succession) of clear-cut areas has been intensively studied (e.g., Bormann and Likens, 1979). However, caution needs to be exercised when translating results of such studies to managed systems, because the regeneration after clear-cutting



Fig. 1. Two systems (smooth line = A and dashed line = B), are assumed to reside in equilibrium and then disturbed. In this case, A and B are both assumed to return to equilibrium, but A does so within a much shorter period of time than does B, at the expense, however, of a much larger deviation from equilibrium. A, because of its swift return, is more elastic than B. On the other hand, there might be societal reasons to perceive the effect on B as less damaging–whereas it returns more slowly it does so with a smaller deviation from equilibrium. Note that the above case is designed such that the integrals of the respective displacements (the shaded areas) are equal. The shaded areas might, for instance, represent loss of biomass, carbon-sink capacity, fibre quality, biodiversity, or aesthetic values, in a forest system. A policymaker would then, through weighting, clarify (and have to explicitly motivate) which behaviour would be seen as less damaging. In principle, the problem can be seen as one of optimisation (or cost-benefit analysis) also involving discounting.

is made from plantation and not (for the managed plant species) from seed or seedling banks, or dispersal. In regard to forest fires, when their perturbation to a managed forest is small, it may be allowed to regenerate naturally. But when a disturbance is large enough to be "stand-replacing" the forest usually is not allowed to regenerate naturally and then seed banks and seed dispersal become less important to the resilience and elasticity of the forest. The soil properties are affected by the character of the fire. If the ground is dry, a large extent of the humic layer can be burned. Mineral soil then becomes exposed, generally increasing the possibility for tree seedlings to grow (Niklasson and Nilsson, 2005, p. 115). In the case of less intense groundfire the rhizomes from the undergrowth will survive and quickly reestablish. Properties affecting the intensity of groundfire may therefore be of importance for the resilience and elasticity of forests disturbed by fire.

3.5. The use of the resistance concept in forest management

The most common stability concept used and studied in forest management is resistance, i.e., the ability of the ecosystem to withstand a given disturbance (and thus not change as a result of the impact). For examples of illustrative case studies wherein stability concepts such as resistance have been applied see Brang (2001), who studied the vulnerability of mountainous forests to disturbance caused by snow and other meteorological and topographical factors. The most important disturbances in relation to resistance are windfalls, fires, insects, and pathogens.

3.5.1. Windfalls

Forest stands can be more or less resistant against windfellings and breakings. The resistance is dependent on the management strategy for the stand, but, regardless of strategy, the trees need to have well-developed root systems in order to withstand strong winds (Cameron, 2002). If subjected to wind stress, trees have been shown to adapt their roots and stems against overturning and breakage (Gardiner et al., 2000). Therefore, stands that have not been subjected to wind stress (and that therefore are less adapted) will be sensitive to wind damage if exposed to a new wind regime (such as might be the result of meteorological change as a manifestation of a shift in climate). This is the case of recently thinned stands or stands adjacent to recently clear-cut areas (Gardiner et al., 2000; Blennow and Sallnäs, 2004). Tree properties that cause an increased vulnerability to wind, with ensuing damage, are: increasing stand height; increasing crown-to-stem weight ratio; decreasing stem diameter; and decreasing stem taper (Cameron, 2002). Also, it has been shown that fertilisation treatments cause an increased growth in the upper crown and that this increase leads to decreased resistance to wind damage (Mitchell, 2000). Some tree species seem to be less resistant to wind-damage, among them are: aspen, spruce, and birch (Ulanova, 2000). It has been suggested that irregular stands would be more windfirm than regular stands, and the main reasons for this would be that the dominant trees in irregular

stands would have more favourable height-to-diameter ratios (Mason, 2002). Management options to create larger spacing between trees include initial spacing, and different thinning strategies (such as different types of selective thinning and systematic thinning) (Cameron, 2002). Wider-than-normal spacing at establishment may lower the structural performance of the timber, however; delayed thinning or selective thinning will create stands vulnerable to wind. Early selective thinning will increase the stand's resistance to wind stress but these methods give very low financial surplus (Cameron, 2002).

What management strategy that should be chosen depends on the amount of wind stress that the stand is and will be subjected to, a choice thus directly relating to the probability and credibility of scenarios for future climatic shifts and their ensuing effects on meteorological parameters and their frequency distributions. At low wind stress a delayed thinning strategy can be used. At medium wind stress selective thinning is suggested and at high wind stress a no-thinning strategy is preferred (Mason, 2002; Cameron, 2002). However, a nothinning strategy leads to an irreversible option; once that strategy has been chosen, thinning cannot be made without seriously decreasing the stand's resistance to wind-stress.

The tree properties that are important to the resistance against wind disturbance (such as height/diameter ratios and crown size) also play an important role for the resistance against damage caused by snow accretion (Kato and Nakatani, 2000).

3.5.2. Forest fires

Fire can be a large-scale disturbance to a forest ecosystem (e.g., Perry, 1994, p. 103). The causes of forest fires are both natural (such as from lightning) and human-induced (from inadvertent spreading of clearance fires and other accidental causes) (Niklasson and Nilsson, 2005, pp. 112–113). Most fires are caused by people, directly or indirectly (FAO, 2005). The interactions involved are complex, however; fire occurrence and severity result from complicated feedbacks between fuel (in terms of biomass), topography, ignition mechanisms, and weather conditions in a given area. Weather conditions such as temperature and precipitation determine the state of the fuel and are thus the key factors for initialising forest fire. Once the fire has started, wind speed and direction are important factors in determining the fire type and its spread. It should be observed that forest fires have increased on a global scale over the past 100 years (Langley Research Centre, 2001).

The implications of stability concepts for forest fire are less straightforward than for wind disturbances. One can manage the forest so as to reduce the number of disturbances (*inter alia*, through reducing the risk of ignition and/or introducing fire fighting schemes), lessen the possibilities for spreading, or lower the fire intensity. There are several management strategies that could change the character of forest fires. In order to reduce their spreading one can remove surface fuels (so as to reduce potential flame length); increase the height to the live crown (which means a longer flame is required for torching); or decrease crown density (to make tree-to-tree crown fire less probable) (Brown et al., 2004). However, increasing height-to-crown ratios and decreasing crown density can cause increased surface wind speed (causing faster spreading of ground fire), and decreasing crown density can also lead to drier surface fuel (Brown et al., 2004). An inverse relationship between fire intensity and fire frequency seems to be an essentially accepted fact (Perry, 1994, p. 110). Whether a fire that burns often but with low intensity is more resistant to forest fires than is a forest that burns more seldom but with larger intensity is open to debate.

3.5.3. Insects and pathogens

Among insects that forage on coniferous trees are Ips typographus on spruce, and different species of Neodiprion and Diprion on pine, and on deciduous trees Tortix viridana, Operopthera brumata and Erannis defoliara (Niklasson and Nilsson, 2005, p. 110). Normally, insects only attack or kill old and weak trees but some species are known to cause severe damage to entire forest stands, such as the spruce budworm Choristoneura fumiferana foraging on balsam fir and white spruce stands in the northern US and Canada (Ludwig et al., 1978; Frelich, 2002, p. 29). Pathogens can have the same effect, also killing weak and old trees. Factors that cause trees to lose resistance to insects and pathogens are insufficiency of nutrients, soil degradation or pollution (Perry, 1994, pp. 481-482) although the relationships between the processes causing the decrease in resistance and the disturbing are rarely straightforward (Andersson et al., 2000). The resistance to large outbreaks of insects and pathogens is dependent on the heterogeneity of the forest landscape. What type of heterogeneity that is most important depends on the insect or pathogen in question. Some insects are species-specific and therefore a mixed species forest is more resistant to an outbreak while others only attack trees of a certain age class and therefore heterogeneity of age classes is more important (Perry, 1994, p. 530).

3.6. Interactions amongst disturbances

Above (Section 3.1) we discussed press disturbances (such as pollution and climate change) as agents that can reduce the resistance of a stand to a particular pulse-type disturbance. From the above analysis, it is obvious that there are also interactions between pulse disturbances. For example, large windfellings can create conditions that will support large fires, and wildfires and insect outbreaks will make trees more susceptible to blowdown (Frelich, 2002, pp. 36-37). Clearly, this example points to a fundamental type of risk-assessment challenge to forestry, inasmuch conflicting strategies are required to enhance stability in terms of resistance. Perceived from a management point of view, however, there might be possibilities for multiple-gain strategies; for instance, enhancing properties that provide stabilisation against wind-felling can simultaneously increase stabilisation against expansion of fires.

4. Ways towards developing new management strategies

Our analysis above shows that several categories of "toolboxes" are needed for seeking out overarching policies

for enhancing stabilising characteristics of managed forests. Among these categories are emulation, adaptive approaches, modelling, and expert judgment.

4.1. Emulating natural disturbance regimes

In recent years, mimicking natural disturbance as a management strategy has been discussed as a means towards creating more sustainable forests (Landres et al., 1999; Niemelä, 1999; Bengtsson et al., 2000; Harvey et al., 2002; Seymour et al., 2002). The arguments for doing so are several (cf., e.g., May, 1975) but the main line of thought is that this would create more heterogeneous stands. Such stands are conceived to be more biodiverse than homogeneous ones and also more "stable" (Frelich, 2002, p. 202). Theory-based counter-arguments are of two kinds. First, logging is never a natural disturbance inasmuch biomass is removed from the forest whereas natural disturbances generally leave more residual organic matter (Bengtsson et al., 2000). Second, forest fires and windstorms normally have a different periodicity than has timber harvesting, and create heterogeneity of a different type (Niemelä, 1999).

Nevertheless, the natural variability of forest ecosystems and of their physical (and chemical) environments is of clear interest as a starting point (Landres et al., 1999); to that end, historical data of the disturbance regimes of the area are required. However, within a framework of a changing climate, such site- or area-specific historical data certainly need to be complemented by data from *other* areas which have been, or are, subject to meteorological regimes of the type assumed probable for the specific area for which better management strategies are being explored for the future. Thus, disturbanceemulation strategies need to put much effort into seeking out and analysing forest systems that can function as proxies with respect meteorological patterns as well as essential components in the forest community for which management scenarios are being developed.

4.2. Adaptive management

In view of the needs for forest management to cope with uncertainties about disturbances, the concept of adaptive management (Walters and Holling, 1990) seems to hold good promise. Here, depending on the purpose of the management plan, stability concepts may play a role, inasmuch adaptive management is seen as an "organised learning by doing" where a canvass of management strategies is explored by scientists, foresters and stake-holders in interaction. Methodologically, the concept draws on simulation models and implementation of large-scale management experiments based on the insights from the modelling exercises (Gallopin, 2004), much in lieu with principles suggested, and in some respects successfully applied, already in the 1970s by Holling (1978).

Walters and Holling (1990) suggest three different forms of adaptive management: "active adaptive management", "passive adaptive management", and "adaptive management as documented trial and error". Active adaptive management includes the process of identifying imaginative policy options, assessing model system performance, identifying gaps of knowledge, designing management actions that fill gaps, including reference areas, implementing actions, measuring performance and choosing best policy options (Meffe et al., 2002, pp. 95–111). Active adaptive management also includes feedbacks amongst these steps. In passive adaptive management the components are omitted that involve construction of elaborate models, or selection of sites for management experiments non-randomly (Meffe et al., 2002, pp. 103–106). In the trial and error version of adaptive management, strategies may be haphazard but later choices are built on lessons learned from the management exercises (Walters and Holling, 1990).

Performing adaptive management may however not be a simple task. Experiments can be considered too costly or risky (Gallopin, 2004). Meffe et al. (2002, p. 108) have listed ecological, socio-economic, and institutional conditions that need to be met in order to create a successful adaptive management strategy. Critics of adaptive management point to the lack of successful schemes reported in the literature. Bormann and Kiester (2004) suggest what they call "Options Forestry" to be a better forest management strategy when planning for a more uncertain future. "Options Forestry" is based on "embracing uncertainty, diversifying management, speeding learning and redefining roles and responsibilities" (Bormann and Kiester, 2004). Although slightly different, the adaptive management approach and the "Options Forestry" idea both include multiple-management strategies and also a certain extent of "learning by doing". We believe that our suggestion above (Section 4.1) with respect to "learning from proxies" can provide additional effectiveness to adaptivemanagement strategies under climate-change uncertainties.

4.3. Modelling

In order to adapt forest management to present or expected disturbances, mechanistic process models can be used. Singledisturbance models, such as addressing critical levels of wind (e.g., Gardiner et al., 2000; Blennow and Sallnäs, 2004; Achim et al., 2005) or snow-accretion (Kato and Nakatani, 2000), include parameters such as tree height, breast height diameter, spacing, crown depth, crown width, root depth, root width, and soil density. Other types of models build on risk probabilities based on measured data (e.g., Pukkala, 1998). In addition, process models developed for other purposes, such as with respect to atmosphere/canopy interactions, and their particular characteristics at forest edges (Wiman and Ågren, 1985), may well be applied to help solve management problems with respect to atmospheric influx of episodically high concentrations of harmful substances, such as carried by fog, or of airborne pathogens.

In the broader context of the needs for developing ecological theory, and its uses in ecosystem models, we observe that mainstream ideas still do not take spatial structure into account. Thus, theory approaches at the system level are still prone to mainly addressing averages of population dynamics parameters, and averages of ambient biotic and abiotic conditions (an approach known as "the mean-field assumption in ecology"; cf., Dieckmann et al., 2000). Stochasticity added to these models (in the population parameters or as added external stochastic forcings) tends to introduce instabilities (DeAngelis and Waterhouse, 1987). Jansen and de Roos (2000) address several aspects of how the dynamics and stochasticity of local populations can be linked to give different large-scale dynamics, including damped oscillations on the large-scale spatial level. More precisely, oscillations in spatially averaged densities become reduced because of oscillation-amplitude damping in the transition regions between local patches containing the populations, and because of phase differences in the oscillations occurring in the patches. Hence, if "mean-field assumptions" are abandoned or at least complemented with richness in space and age distributions, stability, and diversity might well begin to take on significantly more relevant meanings in applied ecology, and thus also in forestry.

4.4. Expert judgment

Another management option is to use expert judgment in assessing stand stability. In a study by Herold and Ulmer (2001), foresters were asked to assess the most important hazards, then to rank the importance of different stand attributes in relation to the most important hazard. Different stands were then ranked according to the probability of damage. This technique seemed to "describe correctly, although not precisely, the risk situation in a stand" (Herold and Ulmer, 2001). However, there was almost no relationship between the assessed stand stability and the explanatory variable (stand attribute). Also on a broader geographical scale, expert assessments of vulnerabilities are being made, based on ecosystem models, scenarios of climate and land-use change, and dialogues with stakeholders (Schröter et al., 2005). Given that judgment of local risks to forestry can make a rendez-vous with such larger-scale assessments, more efficient "toolboxes" for policy-making in forestry may well develop.

Even if there exists one best management option to best preserve the resistance of a forest ecosystem with respect to current and future disturbances, the cost may be out of proportion to the economic gain from the increased stability. Economic factors may be included in forestry models in a probabilistic way (Kangas and Kangas, 2004) and alternatives to managing forests to reduce risk can be the acceptance of loss or attempts to share loss (Gardiner and Quine, 2000). Clearly, issues of discount rates (e.g., NAS, 1992, p. 535) or insurance would typically enter into risk assessment and reduction of the kind implied here.

5. Conclusions

Stability concepts are of great relevance to forest management, but, as argued in this article, these concepts are only relevant if addressed in a framework involving disturbance regimes. In some cases, stability concepts have been used when trying to assess the effects of a particular disturbance. The concepts that have been used are the ones that most easily can be compared with a reference state (resistance, resilience, and elasticity) and the most studied disturbances are the ones which are relatively discrete in time (wind, forest fire, insects, and pathogens). When doing so, a straightforward question is being addressed that relatively easily can be tested, and results can be compared between sites and species. When making decisions about forest management strategies connected to elasticity, expert weighting of the type of recovery from a disturbance might be a useful tool.

In some studies the stability of species composition (instead of for instance plant biomass) is investigated. This is of importance for conservation purposes, but to forestry the stability of the standing biomass, or even more relevantly the stability of the economic yield, is a major concern.

Since it seems highly unlikely that there exists one strategy option that can optimise for all types of disturbances and that also can maximise for all other demands placed on a forest (such as with respect to atmospheric carbon sequestration, biodiversity, recreation functions) the management of forests has to be related to the most relevant disturbances (given risks for, and frequencies of, relevant disturbances can be adequately assessed). If the uncertainties are large, then the optimal forest management strategy (even for a small set of forest ecosystem services) may not be found. In that case a multitude of management options may be combined as an insurance strategy. This may work with forest owners possessing large forest areas, but with small-scale forest owners such management schemes would probably need to be combined with some kind of burden sharing, since forest management strategies might be connected with an increased risk and/or increased costs.

Possibly, heterogeneous/mixed forest communities could also safeguard against climate variability with ensuing uncertainty in the frequency and amplitude in meteorological parameters. This would then work as an insurance also against uncertain future disturbances that are not, or only indirectly, related to climatic change. However, whether enhancing forest heterogeneity would provide stabilising mechanisms (such an increased resistance) needs empirical testing and/or in-depth analysis of existing case studies. Moreover, if models are to be used in scenario-making of future changes in disturbance more knowledge has to be gained about the mechanisms of disturbance and how different management strategies will affect the resistance to various types of disturbance. Steps towards spatially resolved vulnerability assessment of regions in Europe are now being taken in scenario-making of the effects of a set of driving forces, including climate change (Schröter et al., 2005). Forest management - in Sweden, Europe, and elsewhere - undoubtedly will become an increasingly crucial component in responding to the potentially severe changes in meteorological and hydrological regimes. For instance one might speculate that fundamental shifts with respect to choice of tree species (such as deciduous instead of coniferous species) might become necessary in long term management strategies, in contrast to short term tactical practices.

Management in relation to disturbance could either be specific (in case of a single, discrete, and predictable disturbance) or be of the insurance type (in case of multiple, unpredictable disturbances), such as using adaptive management. We also note the importance of spatial scale when relating disturbance to stability. Further research and model developments are needed in this area.

Acknowledgements

This work was funded by the Faculty Board of Natural Sciences and Technology at Kalmar University, Sweden. We would like to thank Eva Lövbrand, Ausra Reinap, Göran I. Ågren and two anonymous reviewers for constructive criticism of earlier versions of this paper. It draws on a presentation made at the conference: "Bridging the Gap—policies and science as tools in implementing Sustainable Forest Management", October 17–19/21, 2005, Alnarp, Sweden.

References

- Achim, A., Ruel, J.-C., Gardiner, B.A., Laflamme, G., Meunier, S., 2005. Modelling the vulnerability of balsam fir forests to wind damage. Forest Ecol. Manage. 204, 35–50.
- Andersson, F.O., Ågren, G.I., Führer, E., 2000. Sustainable tree biomass production. Forest Ecol. Manage. 132, 51–62.
- Bäckstrand, K., Lövbrand, E., 2006. Planting trees to mitigate climate change. Contested discourses of ecological modernization, green governmentality and civic environmentalism. Glob. Environ. Chang. 6, 50–75.
- Begon, M., Harper, J.L., Townsend, C.R., 1986. Ecology. Blackwell Science Ltd., Oxford.
- Bengtsson, J., 1998. Which species? What kind of diversity? Which ecosystem function? Some problems in studies of relations between biodiversity and ecosystem function. Appl. Soil Ecol. 10, 191–199.
- Bengtsson, J., Nilsson, S.G., Franc, A., Menozzi, P., 2000. Biodiversity, disturbances, ecosystem function and management of European forests. Forest Ecol. Manage. 132, 39–50.
- Bengtsson, J., Angelstam, P., Elmqvist, T., Emanuelsson, U., Folke, C., Ihse, M., Moberg, F., Nyström, M., 2003. Reserves, resilience and dynamic landscapes. Ambio 32, 389–396.
- Blennow, K., Sallnäs, O., 2004. WINDA—a system of models for assessing the probability of wind damage to forest stands within a landscape. Ecol. Model. 175, 87–99.
- Bodin, P., Wiman, B.L.B., 2004. Resilience and other stability concepts in ecology: notes on their origin, validity and usefulness. ESS Bull. 2, 33–43.
- Bormann, F.H., Likens, G.E., 1979. Pattern and Process in a Forested Ecosystem. Springer, New York.
- Bormann, B.T., Kiester, A.R., 2004. Options forestry—acting on uncertainty. J. Forest. 102, 22–27.
- Brang, P., 2001. Resistance and elasticity: promising concepts for the management of protection forests in the European Alps. Forest Ecol. Manage. 145, 107–119.
- Brown, R.T., Agee, J.K., Franklin, J.F., 2004. Forest restoration and fire: principles in the context of place. Conserv. Biol. 18, 903–912.
- Cameron, A.D., 2002. Importance of early selective thinning in the development of long-term stand stability and improved log quality: a review. Forestry 75, 25–35.
- Ciais, Ph., Reichstein, M., Viovy, N., Granier, A., Ogée, J., Allard, V., Aubinet, M., Buchmann, N., Bernhofer, Chr., Carrara, A., Chevallier, F., De Noblet, N., Friend, A.D., Friedlingstein, P., Grünwald, T., Heinesch, B., Keronen, P., Knohl, A., Krinner, G., Loustau, D., Manca, G., Matteucci, G., Miglietta, F., Ourcival, J.M., Papale, D., Pilegaard, K., Rambal, S., Seufert, G., Soussana, J.F., Sanz, M.J., Schulze, E.D., Vesala, T., Valentini, R., 2005. Europe-wide reduction in primary productivity caused by the heat and drought in 2003. Nature 437, 529–533.

- DeAngelis, D.L., Waterhouse, J.C., 1987. Equilibrium and nonequilibrium concepts in ecological models. Ecol. Monogr. 57, 1–21.
- De Grandpré, L., Bergeron, Y., 1997. Diversity and stability of understory communities following disturbance in the southern boreal forest. J. Ecol. 85, 777–784.
- Dieckmann, U., Law, R., Metz, J.A.J. (Eds.), 2000. The Geometry of Ecological Interactions. Simplifying Spatial Complexity. Cambridge University Press, Cambridge.
- Dorren, L.K.A., Berger, F., Imeson, A.C., Maier, B., Rey, F., 2004. Integrity, stability and management of protection forests in the European Alps. Forest Ecol. Manage. 195, 165–176.
- Ehrlich, P., Ehrlich, A., 1981. Extinction—The Causes and Consequences of the Disappearance of Species. Ballentine Press, New York.
- Elton, C.S., 1958. The Ecology of Invasions by Animals and Plants. University of Chicago Press, Chicago and London.
- FAO, 2005. Global Forest Resources Assessment 2005 Progress towards sustainable forest management. FAO Forestry Paper 147, Food and Agriculture Organisation, United Nations, Rome.
- Farrell, E.P., Führer, E., Ryan, D., Andersson, F., Hüttl, R., Piussi, P., 2000. European forest ecosystems: building the future on the legacy of the past. Forest Ecol. Manage. 132, 5–20.
- Frelich, L.E., 2002. Forest Dynamics and Disturbance Regimes. Cambridge University Press, Cambridge.
- Führer, E., 2000. Forest functions, ecosystem stability and management. Forest Ecol. Manage. 132, 29–38.
- Gallager, R.G., 1968. Information Theory and Reliable Communication. Wiley, New York.
- Gallopin, G.C., 2004. What kind of system of science (and technology) is needed to support the quest for sustainable development? In: Schellnhuber, H.J., Crutzen, P.J., Clark, W.C., Held, H. (Eds.), Earth System Analysis for Sustainability. The MIT Press, Cambridge, pp. 367–386.
- Gardiner, B.A., Quine, C.P., 2000. Management of forests to reduce risk of abiotic damage—a review with particular reference of strong winds. Forest Ecol. Manage. 135, 261–277.
- Gardiner, B., Peltola, H., Kellomäki, S., 2000. Comparison of two models for predicting the critical wind speeds required to damage coniferous trees. Ecol. Model. 129, 1–23.
- Gardner, M.R., Ashby, W.R., 1970. Connectance of large dynamic (cybernetic) systems: critical values for stability. Nature 228, 784.
- Goodman, D., 1975. The theory of diversity-stability relationships in ecology. Q. Rev. Biol. 50, 237–266.
- Granström, A., 1998. Forest fire and fire management in Sweden. Int. For. Fire News 18, 75–77.
- Grimm, V., Wissel, C., 1997. Babel, or the ecological stability discussions: an inventory and analysis of terminology and guide for avoiding confusion. Oecologia 109, 323–334.
- Haken, H., 1978. Synergetics. Springer-Verlag, Heidelberg.
- Halpern, C.B., 1988. Early successional pathways and the resistance and resilience of forest communities. Ecology 69, 1703–1715.
- Halpern, C.B., 1989. Early successional patterns of forest species: interactions of life history traits and disturbance. Ecology 70, 704–720.
- Harding, S., Ravn, H.P., 1985. Seasonal activity of *Ips typographus* L. (Col., Scolytidae) in Denmark. Z. Ang. Ent. 99, 121–131.
- Harper, J.L., 1977. Population Biology of Plants. Academic Press, London.
- Harper, J.L., Hawksworth, D.L., 1995. Preface. In: Hawksworth, D.L. (Ed.), Biodiversity—Measurement and Estimation. Chapman and Hall, Oxford, pp. 5–12.
- Harper, K.A., Bergeron, Y., Drapeau, P., Gauthier, S., De Grandpré, L., 2005. Structural development following fire in black spruce boreal forest. Forest Ecol. Manage. 206, 293–306.
- Harte, J., 1979. Ecosystem stability and the distribution of communityr matrix eigenvalues. In: Halfon, E. (Ed.), Theoretical Systems Ecology. Advances and Case Studies. Academic Press, New York, pp. 453– 466.
- Harvey, B.D., Leduc, A., Gauthier, S., Bergeron, Y., 2002. Stand-landscape integration in natural disturbance-based management of the southern boreal forest. Forest Ecol. Manage. 155, 369–385.

- Herold, A., Ulmer, U., 2001. Stand stability in the Swiss National Forest Inventory: assessment technique, reproducibility and relevance. Forest Ecol. Manage. 145, 29–42.
- Holling, C.S., 1978. Adaptive Environmental Assessment and Management. Wiley, New York.
- Holling, C.S., 1986. The resilience of terrestrial ecosystems: local surprise and global change. In: Clark, W.C., Munn, R.E. (Eds.), Sustainable Development of the Biosphere. Cambridge University Press, Cambridge, pp. 292–317.
- Holling, C.S., 2001. Understanding the complexity of economic, ecological and societal systems. Ecosystems 4, 390–405.
- Hooper, D.U., Chapin III, F.S., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J., Wardle, D.A., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol. Monogr. 75, 3–35.
- Horn, H.S., 1974. The ecology of secondary succession. Ann. Rev. Ecol. Syst. 5, 25–37.
- Houghton, J.T., Ding, Y., Griggs, D.J., Noguer, M., van der Linden, P.J., Dai, X., Maskell, K., Johnson, C.A., 2001. Climate Change 2001: The Scientific Basis. Cambridge University Press, Cambridge.
- Hulme, M., Carter, T.R., 2000. The changing climate in Europe. In: Parry, M.L. (Ed.), Assessment of the Potential Effects of Climate Change in Europe. The ACACIA Report, pp. 47–84.
- Hüttl, R.F., Schneider, B.U., 1998. Forest ecosystem degradation and rehabilitation. Ecol. Eng. 10, 19–31.
- Jansen, V.A.A., de Roos, A.M., 2000. The role of space in reducing predatorprey cycles. In: Dieckmann, U., Law, R., Metz, J.A.J. (Eds.), The Geometry of Ecological Interactions. Simplifying Spatial Complexity. Cambridge University Press, Cambridge, pp. 183–201.
- Jönsson, A.M., 2004. Klimatet och risken för angrepp av granbarkborre (in Swedish). In: Blennow, K. (Ed.), Osäkerhet och aktiv riskhantering-Aspekter på osäkerhet och risk i sydsvenskt skogsbruk, SUFOR, Lund, pp. 45–50.
- Kangas, A.S., Kangas, J., 2004. Probability, possibility and evidence: approaches to consider risk and uncertainty in forest decision analysis. Forest Policy Econ. 6, 169–188.
- Kareiva, P., 1987. Habitat fragmentation and the stability of predator-prey interactions. Nature 326, 388–390.
- Kareiva, P., Wennergren, U., 1995. Connecting landscape patterns to ecosystem and population processes. Nature 373, 299–302.
- Karnosky, D.F., Percy, K.E., Thakur, R.C., Honrath, R.E., 2003. Air pollution and global change: a double challenge to forest ecosystems. In: Karnosky, D.F., Percy, K.E., Chappelka, A.H., Pikkarainen, J. (Eds.), Air Pollution, Global Change and Forests in the New Millenium. Elsevier, Amsterdam, pp. 1–41.
- Kato, A., Nakatani, H., 2000. An approach for estimating resistance of Japanese cedar to snow accretion damage. Forest Ecol. Manage. 135, 83–96.
- Kazanis, D., Arianoutsou, M., 2004. Long-term post-fire vegetation dynamics in *Pinus halepensis* forests of Central Greece: a functional group approach. Plant Ecol. 171, 101–121.
- Landres, P.B., Morgan, P., Swanson, F.J., 1999. Overview of the use of natural variability concepts in managing ecological systems. Ecol. Appl. 9, 1179– 1188.
- Langley Research Centre—NASA, 2001. Biomass Burning: A Hot Issue in Global Change. FactSheet FS 2001-02-56-LaRC.
- Larsen, J.B., 1995. Ecological stability of forests and sustainable silviculture. Forest Ecol. Manage. 73, 85–96.
- Lashof, D.A., Ahuja, D.R., 1990. Relative contributions of greenhouse gas emissions to global warming. Nature 344, 529–531.
- Lawton, J.H., 1994. What do species do in ecosystems? Oikos 71, 367-374.
- Leps, J., 2004. Variability in population community biomass in a grassland community affected by environmental productivity and diversity. Oikos 107, 64–71.
- Leps, J., Brown, V.K., Diaz Len, T.A., Gormsen, D., Hedlund, K., Kailová, J., Korthals, G.W., Mortimer, S.R., Rodriguez-Barrueco, C., Roy, J., Santa Regina, I., van Dijk, C., van der Putten, W.H., 2001. Separating the chance

effect from other diversity effects in the functioning of plant communities. Oikos 92, 123–134.

- Loreau, M., 2000. Biodiversity and ecosystem functioning: recent theoretical advances. Oikos 91, 3–17.
- Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., Tilman, D., Wardle, D.A., 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294, 804–808.
- Lotka, A.J., 1956. Elements of Mathematical Biology (earlier published as: Lotka, A.J., 1924. Elements of Physical Biology). Dover publications Inc., New York.
- Ludwig, D., Jones, D.D., Holling, C.S., 1978. Qualitative analysis of insect outbreak systems: the spruce budworm and forest. J. Anim. Ecol. 47, 315– 332.
- Mason, W.L., 2002. Are irregular stands more windfirm? Forestry 75, 347-355.
- May, R.M., 1972. Will a large complex system be stable? Nature 238, 413–414.
 May, R.M., 1973. Stability and Complexity in Model Ecosystems. Princeton University Press. Princeton.
- May, R., 1975. Stability in ecosystems: some comments. In: van Dobben,
 W.H., Lowe-McConnell, R.H. (Eds.), Unifying Concepts in Ecology. Dr.
 W. Junk B.V. Publishers, The Hague, pp. 161–168.
- May, R.M., 1999. Unanswered questions in ecology. Philos. T. Roy. Soc. B 354, 1951–1959.
- McCann, K.S., 2000. The diversity-stability debate. Nature 405, 228-233.
- Meffe, G.K., Nielsen, L.A., Knight, R.L., Schenborn, D.A., 2002. Ecosystem Management—Adaptive, Community-based Conservation. Island Press, Washington.
- Mitchell, S.J., 2000. Stem growth responses in Douglas-fir and Sitka spruce following thinning: implications for assessing wind-firmness. Forest Ecol. Manage. 135, 105–114.
- Naeem, S., 1998. Species redundancy and ecosystem reliability. Conserv. Biol. 12, 39–45.
- NAS (U.S. National Academic of Sciences), 1992. Policy Implications of Greenhouse Warming. National Academy Press, Washington.
- Niemelä, J., 1999. Management in relation to disturbance in boreal forest. Forest Ecol. Manage. 115, 127–134.
- Niklasson, M., Nilsson, S.G., 2005. Skogsdynamik och arters bevarande (in Swedish). Studentlitteratur, Lund.
- Odum, E.P., 1963. Relationships between structure and function in the ecosystem. Jpn. J. Ecol. 12, 108–119.
- Odum, E.P., 1969. The strategy of ecosystem development. Science 164, 262–270.
- Olofsson, E., Blennow, K., 2005. Decision support for identifying spruce forest stand edges with high probability of wind damage. Forest Ecol. Manage. 207, 87–98.
- Orians, G.H., 1975. Diversity, stability and maturity in natural ecosystems. In: van Dobben, W.H., Lowe-McConnell, R.H. (Eds.), Unifying Concepts in Ecology. Dr. W. Junk B.V. Publishers, The Hague, pp. 139– 150.
- Parry, M.L., 1986. Some implications of climatic change for human development. In: Clark, W.C., Munn, R.E. (Eds.), Sustainable Development of the Biosphere. Cambridge University Press, Cambridge, pp. 378–407.
- Perry, D.A., 1994. Forest Ecosystems. The John Hopkins University Press, Baltimore and London.
- Perry, D.A., Jing, H., Youngblood, A., Oetter, D.R., 2004. Forest structure and fire susceptibility in volcanic landscapes of the Eastern High Cascades, Oregon. Conserv. Biol. 18, 913–926.
- Pimm, S.L., 1984. The complexity and stability of ecosystems. Nature 307, 321–326.

- Pukkala, T., 1998. Multiple risks in multi-objective forest planning: integration and importance. Forest Ecol. Manage. 111, 265–284.
- Rummukainen, M., Bergström, S., Persson, G., Rodhe, J., Tjernström, M., 2004. The Swedish Regional Climate Modelling Program, SWECLIM—a review. Ambio 33, 176–182.
- Schaffer, W.M., Kot, M., 1985. Do strange attractors govern ecological systems? Bioscience 35, 342–350.
- Scheffer, M., Carpenter, S., Foley, J.A., Folke, C., Walker, B., 2001. Catastrophic shifts in ecosystems. Nature 413, 591–596.
- Schläpfer, F., Schmid, B., 1999. Ecosystem effects of biodiversity: a classification of hypotheses and exploration of empirical results. Ecol. Appl. 9, 893–912.
- Schröter, D., Cramer, W., Leemans, R., Prentice, I.C., Araújo, M.B., Arnell, N.W., Bondeau, A., Bugmann, H., Carter, T.R., Gracia, C.A., de la Vega-Leinert, A.C., Erhrad, M., Ewert, F., Glendining, M., House, J.I., Kakaanpää, S., Klein, R.J.T., Lavorel, S., Lindner, M., Metzger, M.J., Meyer, J., Mitchell, T.D., Reginster, I., Rounsevell, M., Sabaté, S., Sitch, S., Smith, B., Smith, J., Smith, P., Sykes, M.T., Thonicke, K., Thuiller, W., Tuck, G., Zaehle, S., Zierl, B., 2005. Ecosystem service supply and vulnerability to global change in Europe. Science 310, 1333–1337.
- Selmants, P.C., Knight, D.H., 2003. Understory plant species composition 30– 50 years after clearcutting in southeastern Wyoming coniferous forests. Forest Ecol. Manage. 185, 275–289.
- Seymour, R.S., White, A.S., deMaynadier, P.G., 2002. Natural disturbance regimes in northeastern North America-evaluating silvicultural systems using natural scales and frequencies. Forest Ecol. Manage. 155, 357–367.
- Shannon, C.E., Weaver, W., 1949. The Mathematical Theory of Communication. University of Illinois Press, Urbana.
- Srivastava, D.S., Vellend, M., 2005. Biodiversity-Ecosystem function research: Is it relevant to conservation. Annu. Rev. Evol. Syst. 36, 267–294.
- Tilman, D., 1999. The ecological consequences of changes in biodiversity: a search for general principles. Ecology 80, 1455–1474.
- Ulanova, N.G., 2000. The effects of windthrow on forests at different spatial scales: a review. Forest Ecol. Manage. 135, 155–167.
- Vlijm, L., Likens, G.E., 1975. Summary of discussion on "diversity, stability and maturity in ecosystems influenced by human activities". In: van Dobben, W.H., Lowe-McConnell, R.H. (Eds.), Unifying Concepts in Ecology. Dr. W. Junk B.V. Publishers, The Hague, pp. 232–236.
- Walker, B.H., 1992. Biodiversity and ecological redundancy. Conserv. Biol. 6, 18–23.
- Walters, C.J., Holling, C.S., 1990. Large-scale management experiments and learning by doing. Ecology 71, 2060–2068.
- White, P.S., Pickett, S.T.A., 1985. Natural disturbance and patch dynamics: an introduction. In: Picket, S.T.A., White, P.S. (Eds.), Natural Disturbance and Patch Dynamics. Academic Press, San Diego, pp. 3–13.
- Whittaker, R.H., 1977. Evolution of species diversity in land communities. Evol. Biol. 10, 1–67.
- Wiman, B.L.B., 1991. Implications of environmental complexity for science and policy. Glob. Environ. Chang. 1, 235–247.
- Wiman, B.L.B., 2002. Effects of global warming on environmental pollution. In: Yotova, A. (Ed.), Natural Resources System Challenge: Climate Change, Humans Systems and Policy, in Encyclopedia of Life Support Systems. Eolss Publishers Co., Oxford Internet at www.eolss.net.
- Wiman, B.L.B., Holst, J., 1982. Ekologisk tolerans—om stabilisering och föränderlighet i ekologiska system (in Swedish). Rapport Nr. 11, Naturresurs-och Miljökommittén, Jordbruksdepartementet (Swedish Ministry of Agriculture), Departementets Reprocentral, Stockholm.(ISSN 0349-2613).
- Wiman, B.L.B., Ågren, G.I., 1985. Aerosol depletion and deposition in forests—a model analysis. Atmos. Environ. 19, 335–347.