Chapter 3

Vulnerability Analysis of Ecological Systems

Carina R. Lalyer, Arnim von Gleich and Bernd Giese

Introduction

Vulnerability analysis can be seen as the counterpart to technology characterization. Technology characterisation scrutinises the intervening technology. Vulnerability analyses potentially affected systems. That may be socio-ecological, socio-technical, socio-economic or other systems. In this chapter ecological systems are in focus.

Ecosystems represent complex assemblies whose dynamics are still far from being fully understood. Modelling the behaviour of ecological systems is thus a challenging task. Extensive abstractions are required to enable the analysis of the performance of at least some of its elements under changing environmental conditions or in the presence of certain stressors. In particular, for “novel entities” (Steffen et al. 2015) like gene drives, an analysis of their possible impact on ecosystems is complicated especially because of the lack of comparative cases. In the course of a vulnerability analysis of an ecosystem affected by gene drives, assessments of potential impacts are only possible in a rather simplified form. As an ecosystem may be defined by the interactions between its biotic and abiotic elements (Chapin et al. 2011, p. 5), the vulnerability analysis of an ecosystem requires an investigation at different hierarchical levels, from species characterization to the organism’s interactions with the environment including its abiotic attributes (De Lange et al. 2010). Elements of these levels as for example species that fulfil important functions like ecosystem engineers, may represent central parts of tipping point dynamics when they are affected above a certain threshold.

C. R. Lalyer (✉) · B. Giese

Institute of Safety/Security and Risk Sciences (ISR), University of Natural Resources and Life Sciences, Vienna (BOKU), Austria

e-mail: carina.lalyer@boku.ac.at

A. von Gleich

Department of Technological Design and Development, Faculty Production Engineering, University of Bremen, Bremen, Germany

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To explore the relevant criteria for a vulnerability analysis of ecosystems that are confronted with a gene drive, a framework for this kind of analysis is developed in this chapter.

Ecosystem Vulnerability Analysis

The technological advances in gene drive systems opened new possibilities for the scientific community, interested parties and governments to address problems in the agricultural, conservation and public health sector. However, these developments are highly debatable. Gene drives can be used to transform, suppress or even eliminate specific species (Meghani and Kuzma 2017) that act as disease vectors, reduce biodiversity or have become agricultural pests. Currently, one of the greatest threats to biodiversity is the establishment of invasive species (Scalera 2010). Known methods to control organisms only lead to a short term suppression of the population and thus rely on continuous applications (Moro et al. 2018). However, using gene drives in wild populations requires careful considerations because the impact of the use of this new technology is far reaching and uncertain.

This uncertainty and lack of knowledge is due to research gaps concerning the biological and ecological traits of certain species and as well as knowledge gaps regarding the ecological effects of hazards and exposure after releasing gene drives (GD) into wild populations (Moro et al. 2018).

Moreover, due to many failures in the attempt to eradicate or control unwanted species,¹ a rigorous study must be performed to assess the potential impacts and risks associated with the unprecedented release of gene drive organisms (GDO). As already mentioned, vulnerability analysis is confronted with different forms of lacking knowledge, with scientific uncertainties, known unknowns and unknown unknowns. Vulnerability analysis may contribute to the reduction of any one of them, by more precise science, by modelling or by identifying tipping points.

An ecological vulnerability analysis is suggested to be applied when a specific threat for the environment is expected (De Lange et al. 2010). For example, exposure of an ecosystem to a threat could be the release of GDs into wild populations. In the light of the potential power and range of current GD systems and regarding the fact that a gradual release approach is impossible, as it is practised with common GMOs, an a priori analysis is necessary to determine how vulnerable an ecosystem is. Essential steps are the identification of its exposure and sensitivity towards such a perturbation, its internal weaknesses and tipping points and its capacity to recover or adapt following an initial perturbation (von Gleich et al. 2010; Gößling-Reisemann et al. 2013; Weißhuhn et al. 2018).

Turner et al. (2003) describe vulnerability as the “degree to which a system, sub-system or system component is likely to experience harm due to exposure to a hazard,

¹E.g. for population control of rabbits (Arthur and Louzis 1988) or the introduction of the cane toad in Australia to protect the cultivation of sugar cane (Doody et al. 2015).

either a perturbation or stress/stressor.” (Turner et al. 2003, p. 8074). “Vulnerability” is used in both social and natural science disciplines, where authors define it in different ways, without a consensus of its conceptualization (Füssel 2007). Newell et al. (2005 cited in Füssel 2007) even suggested that the term vulnerability is a “conceptual cluster” in interdisciplinary research.

Although ecosystem vulnerability is still a new topic, it is important to detect the potential weaknesses and adaptive capacities of an ecosystem under threat (Weißhuhn et al. 2018). Therefore, by performing such an analysis, it should be possible to estimate “the inability of an ecosystem to tolerate stressors over time and space” (Williams and Kapustka 2000, p. 1056).

According to Liverman (1990 cited in Füssel 2007, p. 155) vulnerability is related to concepts of “resilience, marginality, susceptibility, adaptability, fragility and risk” wherein Füssel (2007, p. 155) has added the concepts of “exposure, sensitivity, coping capacity [...] and robustness”. When describing vulnerability, it is important to specify the system and its vulnerability to specific hazards as well as to mention the time frame (Brooks 2003 cited in Füssel 2007, p. 156).

The fundamentals of a vulnerability analysis were set by two “reduced-form models” (Turner et al. 2003, p. 8074) developed in the realm of environmental and climate assessments (White 1974 and Cutter 2001 cited in Turner et al. 2003). First, the risk-hazard model was put into place in the 1970s and 1980s in which the impact of a hazard—the risk—is defined as a function of exposure to the hazard and the “dose–response” (sensitivity) of the system exposed (Burton et al. 1978 and Kates 1985 cited in Turner et al. 2003). Due to the shortcoming of these models, like the lack of taking into account the system’s abilities to amplify or reduce the impacts (Kasperson et al. 1988 and Palm 1990 cited in Turner et al. 2003; Weißhuhn et al. 2018) or the fact that the system comprises different sub-elements that react differently to the hazard (Cutter 1996 and Cutter et al. 2000, cited in Turner et al. 2003; Frazier et al. 2014), the “pressure-and-release” models were developed. In these type of models, risk is defined as a function of stress and the explicit vulnerability of the exposed system (Blaikie et al. 1994 cited in Turner et al. 2003). Although, these models mainly address social vulnerabilities in the face of natural hazards, they put forward the basis of a general vulnerability analysis (Turner et al. 2003). Subsequently, adaptive capacity has been introduced (Smit and Wandel 2006 and Engle 2011 cited in Weißhuhn et al. 2018). Opposed to the history of the concept of vulnerability in which people are susceptible to natural hazards, ecosystem vulnerability analysis follows a view where the environment is exposed to perturbations caused by humans (Birkmann and Wisner 2006; Weißhuhn et al. 2018).

Weißhuhn et al. (2018) performed a review of scientific publications focusing on environmental or ecosystem vulnerability assessments. They found out that this kind of research gained more attention starting from 2009, which denotes a rather new topic in research. Recent work aimed to create a more interdisciplinary framework defining vulnerability as a function of exposure, sensitivity and adaptive capacity (Frazier et al. 2014; Füssel 2007; Weißhuhn et al. 2018). This definition of vulnerability is the framework that is used in the present study.

An ecosystem can be considered vulnerable regarding a certain perturbation when it is highly exposed, has a high sensitivity and low adaptive capacity (Mumby et al. 2014). Thus, those ecosystems that turn out to be vulnerable need proper management strategies (Weißhuhn et al. 2018). According to Weißhuhn et al. (2018) and de Lange et al. (2005, p. 27) *vulnerability* is defined as a function of *exposure* and *sensitivity*, leading to the potential impact (Mumby et al. 2014), and *adaptive capacity* (AC). These qualities will be described in the following passages.

Exposure

Exposure describes the fact that the ecosystem is in contact with the stressor (De Lange et al. 2010). To assess exposure, Frazier et al. (2014) recommend to examine the probability of an occurrence of the disturbance or its spatial proximity, whereas, Dong et al. (2015) suggest to determine the threatened area. The probability of the exposure of an ecosystem towards a certain stressor is determined by the quality of the stressor (e.g. its persistence or pervasiveness) and the qualities of the affected systems. As it is shown in Fig. 3.1, in this study the exposure relevant qualities of the ecosystem are differentiated between qualities of the ecosystem and qualities of the wild species targeted by GDOs. For the latter qualities of the drive have to be taken into account, which influence its spread within and probably also beyond the target species population. The qualities of the drive are identified in the course of the technology characterization as described in Chap. 1. In order to assess the exposure potential of the ecosystem, as suggested by de Lange et al. (De Lange et al. 2010), a possible measurement can be the scale of exposure. In order to determine the scale, the current study has compiled the following characteristics as:

(a) Ecosystem characteristics

1. Distribution of adequate habitat conditions: it is important to know what are the conditions required for the survival of the gene drive target species;
 - The range of environmental characteristics, in which a species lives in, is called the species' ecological niche (Hutchinson 1957 cited in Chase 2011, p. 93). This niche results from evolutionary processes in which species interact with their environment and other organisms (Chase 2011). According to Chase and Leibold (2002 cited in Chase 2011, p. 93) the niche defines a species' spatial existence, biogeography, interspecies interactions, abundance and ecological role. Chase (2011) describes in his review on niche theory, that there are two components in which the definition of a niche can be divided into: first the range of biotic and abiotic characteristics that enable a species to persist in a space (Grinnell 1917; Hutchinson 1957 cited in Chase 2011, p. 94), also named the requirement component (Chase 2011) and secondly, the impact the species has on its given environment (Elton 1927 cited in Chase 2011, p. 94), known as the impact component (Chase 2011).

Fig. 3.1 Relevant criteria and levels of investigation for an event-based analysis of vulnerability (eVA) in adaption to Gößling-Reisemann et al. (2013) and criteria i.e. after de Lange et al. (2010), Moro et al. (2018), Weißhuhn et al. (2018) and Mumby et al. (2014)

- Huey (1991) underlines the importance of the environmental physical conditions (temperature, humidity, salinity etc.) and of the organisms’ physiology to perform in a given habitat or to choose a specific habitat.
- 2. Biogeographical barriers (adapted from Moro et al. 2018);
 - Physical, physiological or environmental barriers influence the dispersal of a species in a certain landscape (Capinha et al. 2015).
 - According to Cox et al. (2016, pp. 91–92), the distribution of species is limited by geographical barriers that can be of different types (e.g. physical like mountains, biological like predators or climatic like temperature etc.).
 - In spite of these natural barriers that have confined species to certain locations, organisms have been able to establish themselves in places far away from their native ranges (Capinha et al. 2015). This “breakdown” of biogeographical barriers arose from human assisted dispersal through travel and trade (Capinha et al. 2015) and causes an intermixing of biota that puts the native species under additional pressure (Capinha et al. 2015; Montgomery et al. 2015). It can be expected that the locations with intensified trading relations and those that are closely located to them will suffer the greatest homogenization of biota (Capinha et al. 2015). The new

biota community would be formed by competitive generalists that will be composed of few but widespread species (McKinney and Lockwood 1999).

3. Distribution of food sources: determines where the organism might migrate;
 - One factor in selecting a habitat is the quality and locality of resources. Habitats undergo fluctuations regarding their quality over time and space (Jonzén et al. 2004). The variation is a consequence of the habitat itself or of the number of organisms using it, in relation to their density (Jonzén et al. 2004).
4. Density of species population;
 - Density-dependent habitat selection portrays the mechanisms behind habitat selection in relation to population size. The size of a population in a certain habitat is bound to density-dependent processes, due to the fact that a population can grow in size as long as the carrying capacity of the habitat allows it (Morris 2003). Fretwell and Lucas (1969 cited in Rosenzweig 1991) suggested that these processes are based on the optimal foraging and intraspecific competition principles.
 - del Monte-Luna et al. (2004, p. 485) propose a general definition of the carrying capacity which is: “the limit of growth or development of each and all hierarchical levels of biological integration, beginning with the population, and shaped by processes and interdependent relationships between finite resources and the consumers of those resources”. The level of limiting resources is not constant over time, it varies according to the stochasticity of the environment, but when abstracted in models, it may be expressed as a fixed parameter (del Monte-Luna et al. 2004).

Qualities of the target species for the gene drive are also highly important to know in order to assess the exposure potential of the GDO. With regard to gene drive-specific qualities, the following list focuses on some points which are also part of the technology characterization of gene drives (see Chap. 1):

(b) Species characteristics

1. Biology and ecology of the target species (adapted from Moro et al. 2018);
2. Habitat choice: different habitats hold different living conditions (adapted from De Lange et al. 2010);
 - Morris (2003) defined habitat selection as the process through which individuals of a certain population preferentially choose to occupy or use a certain habitat based on particular variables. The selection of habitat is related to population density regulation, community interactions and the origin and maintenance of biodiversity (Morris 2003). “Habitat” according to Whittaker et al. (1973 cited in Chase 2011, p. 94) portrays the “environmental features” where a species can live. Whereas in Morris (2003, p. 2) the given definition for habitat is “a spatially bounded area, with a subset of physical and biotic conditions, within which the density

- of interacting individuals, and at least one of the parameters of population growth, is different than in adjacent subsets.”
3. Seasonal influence on the population (adapted from De Lange et al. 2010);
 - Seasonality produces environmental variability in terms of temperature, humidity, resource availability etc. which influences the life-history traits of organisms (Turchin 2003 cited in Taylor et al. 2013).
 4. Gene flow in the target population (adapted from Moro et al. 2018);
 - Moro et al. (2018) argue that the spread of a gene throughout an ideal population is determined by random mating and whether the gene flow is high or not.
 5. Spread rate (invasiveness) of the GD in the target population;
 - In gene drive systems that depend on thresholds, the spread of the GD will be determined not only by its inheritance rate but also by the number of released GDOs. If the necessary ratio of GDO to wild organisms is reached, the GD will spread and GDO numbers will further increase in the long run (Marshall and Akbari 2016).
 6. Ability of dispersal: How far can the organism travel from the source population? (adapted from Moro et al. 2018);
 - This trait of the organism would also determine the gene flow between populations (Mitton 2013; Onstad and Gassmann 2014).
 7. Potential of the GDO to affect non-target populations (adapted from Moro et al. 2018);
 - Gene flow facilitated by dispersal could spread the GD to non-target populations. However, Oye et al. (2014) warn that scientists have little experience with engineering natural systems for evolutionary robustness. Thus, they argue that precision drives could prevent the drive from spreading into non-intended populations, but their reliability requires further research (Oye et al. 2014). Other ways to prevent the spread to other populations than the intended one is by molecular confinement, threshold drives that will not fixate into the population at low frequencies, targeting very specific DNA sequences that are population specific or gene drives that transform the population to be sensible to a specific chemical (Esvelt et al. 2014; Marshall and Akbari 2016; Marshall and Hay 2011).
 8. Potential of the GDO to hybridize (adapted from Moro et al. 2018);
 - Interspecific gene flow may happen through hybridization, introgression (David et al. 2013) or horizontal gene transfer (Werren 2011).

Sensitivity

Sensitivity of the ecosystem is the susceptibility to disturbances (Weißhuhn et al. 2018). It expresses the degree to which the system can be affected by a certain disturbance or stress. It is a quality of the affected system but also depends on

the intensity of the disturbance and may change depending on the length of the exposure due to development of increased tolerance (Weißhuhn et al. 2018). De Lange et al. (2010) emphasise among other aspects the need to know the sensitivity of the community of species, their functions within the ecosystem and the trophic relationships. The following characteristics for sensitivity have been collated on the level of:

(a) Ecosystem characteristics

1. Structural biodiversity (adapted from De Lange et al. 2010), represented by species composition, population structure and number of individuals.
2. Key functional traits of species in the ecosystem: functional role of the species (adapted from De Lange et al. 2010);
 - The dynamics of ecosystems depend on the traits of organisms, their evolutionary histories and interactions in the community (Chapin et al. 2011). Therefore, it is important to understand the role of organisms in their community. Recently, the role of biodiversity in ecosystem functioning has gained popularity and appreciation (Díaz et al. 2006 in Chapin et al. 2011, p. 3).
 - Functional traits represent characteristics that allow a species to survive and reproduce and they impact its fitness. The loss or gain of species within a system can alter ecosystem processes due to the change in the species' functional traits that have great impacts on the system, namely effects on provision or limiting resources, microclimate, intraspecific or interspecific interactions and effects on disturbance regimes (Chapin et al. 2011). It is especially important in case the targeted species is or affects a key stone species (Paine 1969 cited in Bond 1994).
3. Species redundancy within functional groups (difference in sensitivity of functionally similar species) (adapted from De Lange et al. 2010);
 - The redundancy hypothesis suggests that resilience is maintained by the ability of the species to compensate through their functional role in case species are lost (Walker 1992 cited in Mitchell et al. 2000; Fonseca and Ganade 2001).
 - It is thought that the more species are in a system, the wider will be the range of conditions under which ecosystem processes can be maintained at their characteristic state (Chapin et al. 2011). Redundancy denotes diverse responses that allow ecosystem resilience to variation and change (Bengtsson et al. 2003). This is due to the theory of “diversity as insurance” (Chapin et al. 2011): Diversity ensures maintenance of functionality under extreme or novel conditions because different species do not respond in the same way to an eventual perturbation due to their evolution and life history. In other words, species diversity stabilizes ecosystem processes when e.g. annual variations happen or extreme events occur because it is unlikely that all species that perform a functional role go extinct (Walker 1995 in Chapin et al. 2011, p. 333).

4. Trophic relationships within the community (adapted from De Lange et al. 2010);
 - Energy and nutrient flow in an ecosystem is regulated by food webs (Chapin et al. 2011, p. 300). The trophic relationships that determine food webs are complex but can be narrowed down to bottom-up (e.g. productivity of plants regulate herbivore numbers) and top-down controls (e.g. predators that regulate prey population) (ibid.).
5. Emergent properties (adapted from De Lange et al. 2010);
 - According to Reuter et al. (2005), emergent properties are new qualities that form at higher integration levels and constitute more than the sum of the low-level components. The emergence concept is based in a view of nature as a hierarchical structure in which different organizational levels ranging from an individual, to community, ecosystem and landscape exist (Reuter et al. 2005). For example, dispersal characteristics of individuals of different carabid beetles have influence on the population size of these species as an emergent property (ibid.).
6. Seasonal climatic influence (adapted from De Lange et al. 2010)
7. Impact of climate change over time;
 - Can lead to additive effects. An additive effect is when the combined effects of multiple drivers are equal to the sum of the individual effects (Crain et al. 2008). Synergistic cumulative effects occur when the combined effect is greater than the sum of the individual effects (ibid.). Antagonistic cumulative effects occur when the combined effect is smaller than the sum of the individual effects (ibid.).

(b) Species characteristics

1. Genetic diversity of the species;
2. Human pressures on the species;
 - Stressors produced by humans (habitat destruction, hunting, use of pesticides) often interact and produce combined effects on biodiversity or ecosystem services² (Crain et al. 2008), termed additive effects.
3. Influence of climate change (adapted from De Lange et al. 2010).

Adaptive Capacity

The third step in the vulnerability assessment of ecosystems is to investigate their adaptive capacity (AC). According to Weißhuhn, adaptive capacity describes the system's ability to compensate the impacts of disturbances (Weißhuhn et al. 2018). AC is scarcely properly described for natural systems (Weißhuhn et al. 2018), however according to Folke et al. (2002) it is related to genetic diversity, biological diversity

²Ecosystem services are benefits that humans receive from ecological systems (Díaz et al. 2013) e.g. timber, food, biodiversity etc.

and landscape heterogeneity (Peterson et al. 1998; Carpenter et al. 2001; Bengtsson et al. 2003 cited in Folke et al. 2002).

Weißhuhn et al. (2018) suggest that AC can be measured through:

1. Genetic variability (direct relationship)
2. Species ability to reproduce (Díaz et al. 2013 cited in Weißhuhn et al. 2018)
3. Species ability to disperse in/invade into disturbed environments (Díaz et al. 2013 cited in Weißhuhn et al. 2018)
4. Response diversity within functional groups;
 - Elmqvist et al. (2003, p. 488) define response diversity as “the diversity of responses to environmental change among species that contribute to the same ecosystem function.” In order to maintain desirable states of an ecosystem, after a disturbance, it is important that diverse functional groups are available to reorganize the system (Lundberg and Moberg 2003 cited in Elmqvist et al. 2003).

Mumby et al. (2014) highlight the general relevance of biodiversity for the capacity of an ecosystem to adapt. Biodiversity is considered to be the “biological diversity in a system, taking into account the genetic, species diversity and their functional roles but also ecosystem diversity in a landscape” (Chapin et al. 2011). The debate about the role of biodiversity in ecosystem resilience is ongoing.

Event-Based Analysis of Vulnerability

When potential disturbing events can already be described, it is advisable for an analysis of ecosystem vulnerability to refer to the factors exposure, sensitivity and adaptive capacity described in the previous section within the framework of an event-based vulnerability analysis (eVA). In many cases, conclusions about an expected exposure can already be drawn from the character of the disturbance. If, for example, flying insects are considered as the source of the disturbance, a comparatively high mobility and, in the case of distinct climatic tolerance, even ubiquitous distribution and thus intensive exposure can be assumed. An appropriate scheme of an eVA in adaption to Gößling-Reisemann et al. (2013) for the release of GDO is presented in Fig. 3.1.

Potential Tipping Events Caused by GDO

In ecosystems, tipping points can be defined for different dimensions of potential outcomes. Besides a loss of biodiversity by a population reduction, ecosystem functions and services might as well be affected. Moreover, following the disappearance

of a population or a species, functional shifts within the niche of the suppressed species may occur.

In the case of population suppression, tipping points are already reached when the size of the target population is decreased below a certain threshold at which the population becomes instable and potentially disappears. This also applies to non-target species when they are affected due to an interspecific spread of the GD or indirect effects that are caused by the suppression of the target population. An overview on the variety of tipping events that may follow a population suppression is given in Fig. 3.2.

Among the potential impacts of the release of a suppression drive a number of effects represent tipping points. With regard to controllability, a tipping point is already reached when a GD appears in a non-target population. For an application as suppression drive against an invasive species this would mean that it cannot be guaranteed that the drive remains limited to invasive populations. If populations of the target species in their native habitat are also concerned, a suppression might have serious consequences for the respective ecosystem. The worst case would be the eradication of a non-target population, an event that marks a further tipping point in this direction. In general, each local extinction of a target species can be regarded as a tipping event—not least with regard to its potential irreversibility. The final tipping point would then be the global eradication of the target species.

Fig. 3.2 Possible tipping points following a population suppression

Besides an unintentionally strong reduction of the target population with the outcomes as described above, the transfer of a GD from the target species to a non-target species marks an additional dimension of tipping events. Similar to the cases discussed above it may lead to either the eradication of a non-target species population or—as the worst case—to a global extinction of the non-target species.

The extinction of a species on the global or local level may cause different effects within the ecosystem. Adjustments in the abundance and population structure of other species are more distinct if the species that becomes extinct has an important role and therefore a strong interaction with other species as e.g., predator, prey or competitor (Estes et al. 1989). Impacts manifest not only because of the disappearance of a species. Estes et al. recognized that besides global and local extinction also the reduction of a species below a certain level can impede a significant interaction with other species (Estes et al. 1989). They coined the term “ecological extinction” for this class of impairment. Accompanying changes in ecosystem functions and moreover, in ecosystem services would therefore represent tipping points.

With regard to socio-economic systems, the appearance of a new exotic pest or the appearance of a secondary pest due to niche filling after the suppression or eradication of a species denotes a further tipping event.

Structural Analysis of Vulnerability

An event based analysis of the vulnerability of ecosystems, for which the case studies in this volume exemplarily provide preparatory work, will focus on the qualities described above for the characterization of a potential exposure of the system, its sensitivity and adaptive capacity. Still more difficult is the situation when we try not only to consider disturbances that are already known but also unknown perturbations, so-called ecological surprises (Filbee-Dexter et al. 2017). In this case not an event based vulnerability analysis (eVA) but a structural vulnerability analysis (sVA) of the system is the method of choice (Göbbling-Reisemann et al. 2013). The structural vulnerability analysis asks at which elements or relations the system will surrender, when it comes under pressure. The distinction between eVA and sVA additionally meets the requirements of the fact that an ecosystem is not only threatened by external stressors but also by internal stressors, weak points and tipping points. Whereas an eVA is oriented along an analysis of exposure, sensitivity and adaptive capacity of the potentially affected system, the structural analysis excludes exposure and sensitivity and instead focuses on critical elements within the system that primarily account for its vulnerability. With the term critical elements an additional aspect comes into view regarding the ecosystem services of the system. Critical elements refer to elements that are essential (of high value) for the society that is dependent on the systems services (e. g. feed or food, healthy air and water etc.). Independent of any external perturbations, the specific condition and structure of potentially affected ecosystems yields important information on their general vulnerability. A structural analysis of vulnerability (sVA) lays its focus on the structure and the adaptive capacity of

the system, on its capacities to cope with unknown external stressors, as well as internal weak points, tipping points and critical elements and thus on the capability to maintain system services.

Resilience of Ecosystems

Investigations of inevitable competencies, construction elements and construction principles of systems for their resilience yielded adaption and resistance (or robustness) as necessary abilities and (e.g.) redundancy, diversity and self-organization as important construction principles (von Gleich and Giese 2019). Although different authors define adaptive capacity as either “potential of recovery” or “resilience” (Weißhuhn et al. 2018), both of the concepts are being characterized by the ecosystem’s biotic elements (Oliver et al. 2015; Thrush et al. 2009; Weißhuhn et al. 2018). But apart from a confusing mixture of the concept of resilience with the capacity to adapt (as an element of vulnerability analysis), the full potential of resilience can only be tapped when both terms are applied separately.

Through resilience, ecosystems maintain relatively stable functionality over long periods of time despite fluctuations in the environment. Holling introduced resilience in ecosystem theory as the capacity to “absorb changes of state variables, driving variables, and parameters, and still persist.” (Holling 1973, p. 17). Thereby, resilience determines the persistence of systems—or their extinction. According to Thrush et al. (2009), resilience is the potential for recovery from disturbance (Pimm 1991 cited in Thrush et al. 2009). Holling later referred to this definition of resilience as engineering resilience (Holling 1996). An indicator for engineering resilience is seen in the “duration of the recovery phase” (Weißhuhn et al. 2018). Mitchell et al. (2000) state that an ecosystem returns faster in time to equilibrium after a perturbation when its resilience is high. The second definition is that of the ecological resilience “a variable that represents the movement of an ecosystem within and between stability domains” (Thrush et al. 2009, p. 3209, see also Gunderson 2000; Ludwig et al. 1997; Holling 1996). Walker et al. define ecological resilience as “the capacity of a system to absorb disturbance and reorganize while undergoing change so as to still retain essentially the same function, structure, identity, and feedbacks” (Walker et al. 2004, p. 5). According to Thrush et al. (2009) engineering resilience can be used to measure resilience empirically while ecological resilience requires measurement over a long time period. Besides the differentiation of engineering and ecological resilience, a transition in the notion of resilience occurred in that it was once focused on the conservation of structure integrity and is now also considering reorganization of the affected system (Oliver et al. 2015).

Ecosystems are resilient to regimes of natural variations like daily, seasonal or annual cycles and to extreme events that occurred already throughout their evolutionary history. Positive and negative feedbacks are of high importance to maintain the internal dynamics of an ecosystem (Hanski et al. 2001; Chapin et al. 2011). Negative

feedbacks are the ones that stabilize the system and confer resilience (Chapin et al. 2011).

Oliver et al. (2015) suggest the same characteristics as being descriptive for ecosystem resistance or recovery. They differentiate between the following:

- (a) The level of species:
 - Sensitivity towards change
 - Rate of population increase
 - Adaptive phenotypic plasticity
 - Genetic variability and dispersion (portfolio effect)
 - No growth suppression in the case of low population density (allee effects).
- (b) The level of the communities of species through:
 - Correlation between the traits affected by change and those traits which are important for ecosystem functions
 - Functional redundancy (combined with varying responses to environmental perturbations)
 - Highly connected nested networks of species with generalized interactions versus networks with strong specialized interactions.
- (c) The level of landscapes:
 - Level of heterogeneity in the local environment
 - Landscape level functional connectivity
 - Possibility of alternative stable states
 - Spaciousness which generally promises resource wealth.

In addition, Thrush et al. (2009) stress that resilience is being influenced by:

- Metacommunity structure (pattern of spatial dimensions of specific ecological communities)
- Community connectivity
- β -diversity (quantifies the difference between total species diversity of a region [γ -diversity] and local species diversity [α -diversity] and reflects the species turnover between the different locations in a region).

Moreover, the ecological memory is an important capacity of ecosystems to achieve resilience (Walter et al. 2013 cited in Weißhuhn et al. 2018). The ecological memory shapes how ecosystems react in the face of disturbance regimes and is defined as the “ability of the past to influence the present trajectory of the system” (Peterson 2002 cited in Hughes et al. 2019, p. 40). Depending on the ecological memory which can also be manifested through the species life-history traits or different biotic or abiotic structures like presence of certain species, the ecosystem can be resilient or vulnerable in the face of disturbances (Johnstone et al. 2016).

However, although this listing may be tempting to derive resilience from a mere description of the system under study, Thrush et al. (2009) argues that empirical studies are not sufficient to measure resilience. Instead, there is a need to develop models and identify the positive feedbacks that would drive systems to change.

Regime Shifts and Resilience

The ecological definition of resilience states that a variable of the ecosystem can move “within and between stability domains” (Ludwig et al. 1997 and Gunderson 2000 cited in Thrush et al. 2009). It has been proposed that there is not one stable equilibrium in which the ecosystem can be (Chapin et al. 2011, p. 7) but rather that systems may have alternative stable states reached by abrupt shifts (Oliver et al. 2015) that are determined by large disturbances (Beisner et al. 2003). Alternative stable states have been proposed for the first time in the late 1960s by (Lewontin 1969 cited in Beisner et al. 2003) in reference to communities of organisms (Beisner et al. 2003). According to Beisner et al. (2003), the concept of alternative stable states is being used in ecology in two ways: first, it refers to stability in population ecology (Lewontin 1969 and Sutherland 1974 cited in Beisner et al. 2003). In models of population ecology, the environment is in a fixed state where the biotic community has “different stable configurations” and secondly, the ecosystem perspective focuses on the effects of environmental change (May 1977 cited in Beisner et al. 2003). The variables and characteristics of the communities or ecosystems will persist in different possible arrangements, contributing to an alternate stable state (Beisner et al. 2003).

Therefore, if an ecosystem is resilient, it may enter into an alternative stable state, but if resilience is reduced by for example limiting species redundancy, reducing response diversity or human made pressures, the ecosystem may abruptly shift to a less desirable state (Folke et al. 2004), due to the fact that it may have reached a tipping point. The scientific community still debates when a different state can be named alternative but it is agreed that identification of critical variables and how they are affected requires a thorough understanding of species interactions and feedbacks between the biotic and abiotic elements of the ecosystem (Beisner et al. 2003). Thrush et al. (2009) suggest the following indicators for implications of disturbances or when there is a risk of regime shift (see also Chap. 2 on tipping points for case specific as well as more general indications):

- Communities are homogenising
- The complexities of food webs decrease
- Diversity within functional groups decreases
- Biogenic habitat structure decreases
- Size of organisms decreases
- Decrease in abundance of key species or key functional groups
- Changes in productivity
- Changes in recruitment and juvenile mortality
- Changes in the timing of events which lead to a decoupling of processes.

In order to further unravel the concepts of vulnerability and resilience and at the same time exploit the potential of the latter, it is recommended to shift the use of the resilience concept from an analytical category (related to ecosystem stability or maintenance of ecosystem services) to a guiding concept of the design of resilient socio-ecological systems. In von Gleich and Giese (2019) corresponding construction principles are listed.

Summary

The prospective analysis of the vulnerability of ecosystems is an extremely demanding task considering the necessary knowledge about the elements of an ecosystem and their interaction. According to the current state of research, the vulnerability of an ecosystem is dependent on three main criteria: The magnitude of exposure, the system's sensitivity and its adaptive capacity. Thus, an ecosystem can be considered vulnerable when the magnitude of its exposure is high, its sensitivity is high and its adaptive capacity is low. For each of the three criteria, factors could be identified that significantly influence the impact of a stressor (such as a GDO) on an ecosystem.

In the context of an event-based vulnerability analysis, the categories exposure, sensitivity and adaptive capacity are used to assess the vulnerability of an ecosystem. However, the large number of potentially relevant factors in question can only be partially assessed within the framework of an event based vulnerability analysis.

If an event-based analysis is hindered by lack of knowledge about potential stressors and their possible impacts, a structural analysis of vulnerability can give first hints on weak points, tipping points and critical elements and the general susceptibility of the potentially affected ecosystem to stress. For a structural analysis it is assumed that all elements and relations of the system are subject to stress. The focus is then on the question which of these elements or relations would most likely give way in case of perturbation. Subsequently, it has to be investigated whether a possibility can be identified that a specific stressor like a GDO is able to negatively influence the identified critical elements, relations or weak points.

However, beyond the described indicators that should help to assess the potential vulnerability of an ecosystem, the system's fate is determined by its resilience, a capacity that not only comprises a conservation of structure integrity because it includes the capability for a reorganization of the affected system as well. But reorganization may thereby lead to alternative stable states which may have a less desirable character for humankind.

In the following chapters on case studies some elements of a prospective vulnerability analysis are performed, by the ecological characterisation of olive flies and oilseed rape (also regarding gene flow within and between species) and by the modelling of dispersal and invasiveness. However, these studies can only be seen as preliminary approaches whose value is not least an identification of the knowledge gaps that have to be filled before a more comprehensive analysis of vulnerability is possible.

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